

# CHAPTER 6: PATTERNS OF MAMMAL DIVERSITY

## RESULTS

### *Patterns of Mammal Alpha Diversity*

#### *General Patterns*

Small mammal richness based on Sherman trapping data alone totaled 28 species, and ranged from 2 to 13 species ( $\bar{x} = 7.0$ ,  $SE = 0.27$ ) across all 80 reaches. Richness based on a combination of multiple trapping methods, including Sherman trap, riparian search, pitfall, and point count data, totaled 34 species and one genus (*Lepus* sp.) (Appendix 8), and ranged from 3 to 17 species ( $\bar{x} = 8.8$ ,  $SE = 0.30$ ) per reach. Small mammal richness from Sherman trapping and species richness from multiple methods were highly correlated ( $r = 0.782$ ,  $P < 0.001$ ).

Sampling detected approximately 58% of the species (34 of 59) known to occur in the Lake Tahoe basin. The 25 species not detected consisted primarily of bats ( $n = 10$  species), meso and macro carnivores ( $n = 6$ ), and other larger-bodied, upland species ( $n = 4$ ). I did detect hares, but was not able to distinguish between the 2 potential species in the sighting. However, I detected all but 3 of the 11 riparian-dependent species, of which one (river otter, *Lutra canadensis*) occurs in only one stream, one (muskrat, *Ondatra zibethica*) is associated with standing water only, and one (mink, *Mustela vison*) is unusual in the basin. I also detected all of the riparian-associated mammals except for the bats. Consequently, the results presented here are a relatively thorough representation of riparian-associated species, but do not reflect patterns of association of bats or larger-bodied carnivores.

The 10 most frequently occurring species accounted for approximately 72% of all observations (Fig. 30). Douglas squirrel was the only species detected on every reach, followed closely by deer mouse. Five additional species were present on over 50% of the reaches, including 3 chipmunks, long-tailed vole (*Microtus longicaudus*), and Trowbridge's shrew (*Sorex trowbridgii*).

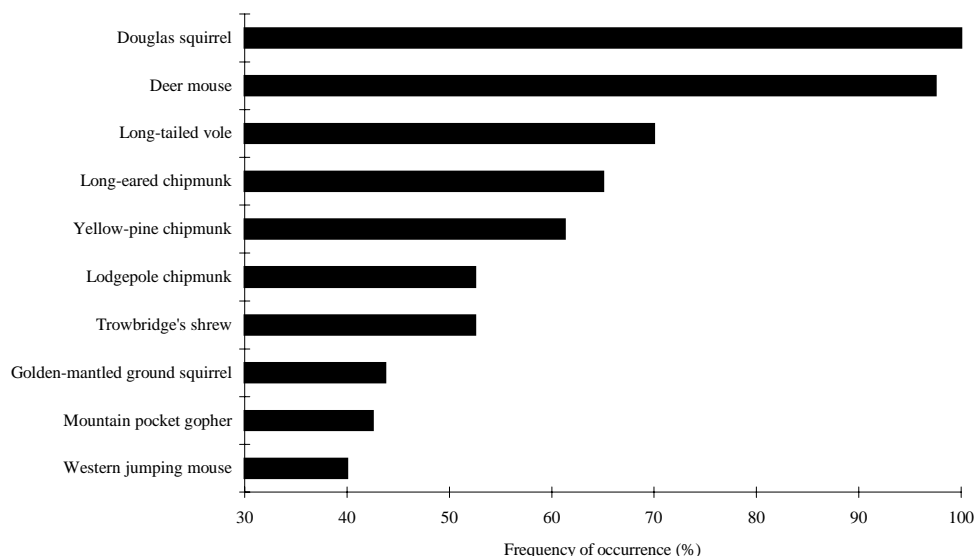


FIG. 30. Ten most frequently occurring mammal species on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

### ***Environmental Relationships of Species Richness***

#### ***Regression Model for Mammal Species Richness***

Mammal species richness was positively correlated ( $P \leq 0.10$ ) with 3 environmental variables, increasing with increases in elevation ( $r = 0.364$ ,  $P = 0.001$ ), aspen–cottonwood ( $r = 0.298$ ,  $P = 0.007$ ), and small logs ( $r = 0.265$ ,  $P = 0.018$ ). Regression of mammal species richness on abiotic environmental variables resulted in a one-variable model: a positive association with elevation (adj.  $R^2 = 0.122$ ) (Table 72). Regression on channel variables resulted no variables being selected. Regression on vegetation variables resulted in a 3-variable model: a positive association with aspen–cottonwood and small logs; and a negative relationship with small snags (adj.  $R^2 = 0.205$ ). Backwards step-wise regression on these 4 key variables resulted in the retention of all 4 variables, so mammal species richness increased with increasing elevation, aspen–cottonwood, and small logs, and decreasing small snags (adj.  $R^2 = 0.256$ ) (Tables 72 and 73).

TABLE 72. Variables selected in step-wise regressions between 3 groups of environmental variables ( $n = 22$ ) and mammal species richness. N = negative association and P = positive association at  $P \leq 0.10$ . Bolded = selected in the final regression at  $P \leq 0.05$  on key variables from each group of environmental variables. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Mammal species richness
<i>Abiotic environment:</i>	
Elevation	<b>P</b>
<i>Vegetation characteristics:</i>	
Aspen–cottonwood	<b>P</b>
Small logs	<b>P</b>
Small snags	<b>N</b>
<i>Variables in final model</i>	<b>4</b>
<i>Adj. <math>R^2</math></i>	<b>0.256</b>

TABLE 73. Final regression model of key environmental variables related to mammal species richness. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Aspen–cottonwood	4.949	1.724	0.281	2.870	0.005
Elevation	8.959	3.608	0.261	2.480	0.015
Small logs	0.433	0.175	0.287	2.470	0.016
Small snags	-0.308	0.140	-0.253	-2.20	0.031

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ( $r = -0.515$ ,  $P < 0.001$ ). It is possible that the positive relationship observed between mammal species richness is a consequence of disturbance being higher at lower elevations. An analysis of covariance with elevation partitioned into 4 groups, and meso-scale disturbance as the covariate

showed that disturbance was not responsible the observed relationship between mammal species richness and elevation (Table 74).

TABLE 74. Analysis of covariance exploring the relationship between mammal species richness and elevation with disturbance as a covariate. SS = sum of squares.  $\nu$  = degrees of freedom. MS = mean square.

Source of variation	SS	$\nu$	MS	F	P
Within + residual	528.40	75	7.05		
Regression	0.20	1	0.20	0.03	0.868
Elevation	44.19	3	14.73	2.09	0.109
Model	53.55	4	13.39	1.90	0.119
Total	581.95	79	7.37		

Graphs of each of the 4 environmental variables against mammal species richness revealed 2 potential environmental thresholds. On reaches with some amount of aspen–cottonwood, a minimum of 6 mammal species were observed (Fig. 31). This indicates that any amount of aspen–cottonwood produces a species richness near or above the average richness occurring across all reaches. Mammal species richness was significantly greater on reaches with aspen–cottonwood (1-tailed test, pooled variance,  $t = 2.38$ ,  $P = 0.016$ ). Additionally, reaches occurring above 2250 m had a minimum of 7 species of mammals (Fig. 32), and mammal species richness was significantly greater on reaches above 2250 m in elevation (1-tailed test, pooled variance,  $t = 2.91$ ,  $P = 0.004$ ).

#### *Mammal Species Richness by Environmental Gradients*

Mammal species richness was positively correlated with the elevation–precipitation and aspen–cottonwood gradients, and negatively correlated with the channel flow gradient (Table 75).

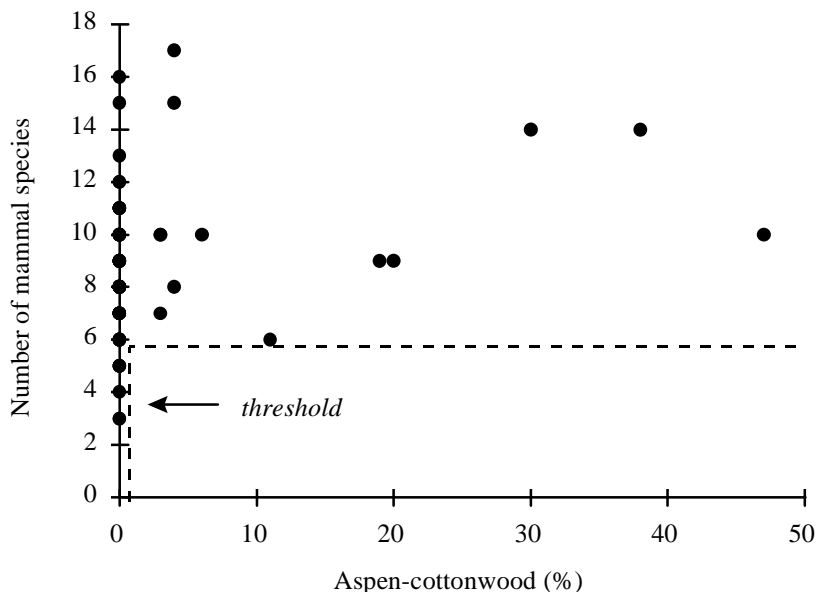


FIG. 31. Threshold between aspen–cottonwood and mammal species richness in the Lake Tahoe basin, 1995 to 1996.

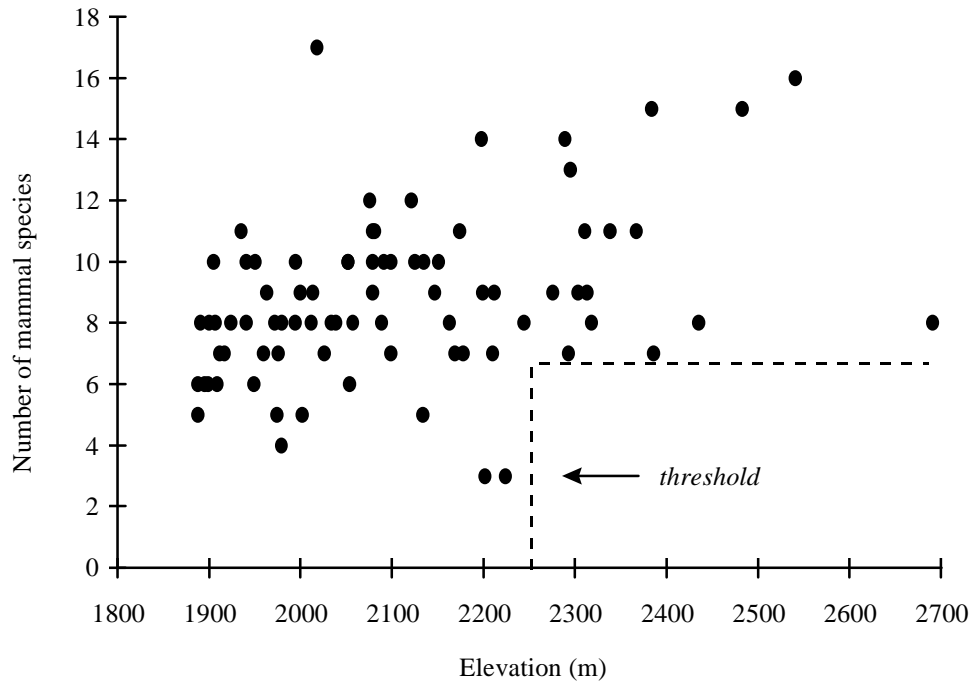


FIG. 32. Threshold between elevation and mammal species richness in the Lake Tahoe basin, 1995 to 1996.

TABLE 75. Correlations between mammal richness and environmental gradients based on principal component analysis. Bolded values indicate  $P \leq 0.10$ . Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Mammal taxonomic richness	
	r	P
<i>Physical gradient:</i>		
1. Elevation–precipitation	<b>0.273</b>	<b>0.014</b>
2. Channel flow	<b>-0.190</b>	<b>0.091</b>
<i>Vegetation gradient:</i>		
1. Forest to meadow	0.007	0.949
2. Subalpine vegetation	0.032	0.776
3. Alder–willow	0.139	0.218
4. Aspen–cottonwood	<b>0.197</b>	<b>0.080</b>
<i>Woody debris gradient:</i>		
1. Snag and log	0.044	0.701

#### *Mammal Species Richness by Basin Orientation*

Mammal species richness varied significantly among orientations ( $v = 3$ , 76;  $SS = 50.62$ , 531.33;  $MS = 16.87$ , 6.99;  $F = 2.41$ ;  $P = 0.073$ ). North ( $\bar{x} = 9.4$ ,  $SE = 0.75$ ) and east ( $\bar{x} = 9.3$ ,  $SE = 0.55$ ) sides of the basin had higher richness than south ( $\bar{x} = 7.2$ ,  $SE = 0.48$ ) and west ( $\bar{x} = 8.8$ ,  $SE = 0.52$ ) sides, but none were significantly different from another (based on Tukey's test).

The east side had the greatest amount of aspen–cottonwood, and aspen–cottonwood was one of the explanatory variables selected in the regression model for species richness. Thus, aspen–cottonwood abundance probably contributed to the higher richness observed on the north and east sides of the basin.

### ***Environmental Relationships of Small Mammal Abundance***

The total number of individuals captured per unit effort of Sherman trapping on each reach ranged from 1.1 to 27.2 individuals/100 trap nights ( $\bar{x} = 9.5$ ,  $SE = 0.66$ ). The most abundant species will make the greatest contribution to total abundance, and therefore environmental relationships will reflect their associations to a greater degree. Of the 35 species, the deer mouse (*Peromyscus maniculatus*) was far more abundant than other mammal species sampled (Fig. 33), constituting 44.6% of all individuals (average abundance = 4.24 indiv/100 trap nights,  $s.d. = 4.03$ ), followed by yellow-pine chipmunk (*Tamias amoenus*) accounting for only 11.1% (average abundance = 1.06 indiv/100 trap nights,  $s.d. = 1.87$ ) of all the individuals. Deer mouse was significantly more abundant than yellow-pine chipmunk ( $v = 112$ ,  $t = 6.409$ ,  $P < 0.001$ , pooled variance), whereas yellow-pine chipmunk was not significantly more abundant ( $v = 120$ ,  $t = 0.96$ ,  $P = 0.17$ , pooled variance) than long-tailed vole, the third most abundant species. Because deer mouse was so much more abundant than the remaining 34 species, I analyzed abundance with and without deer mouse abundance to determine what effect deer mouse had on the observed environmental relationships of mammal abundance.

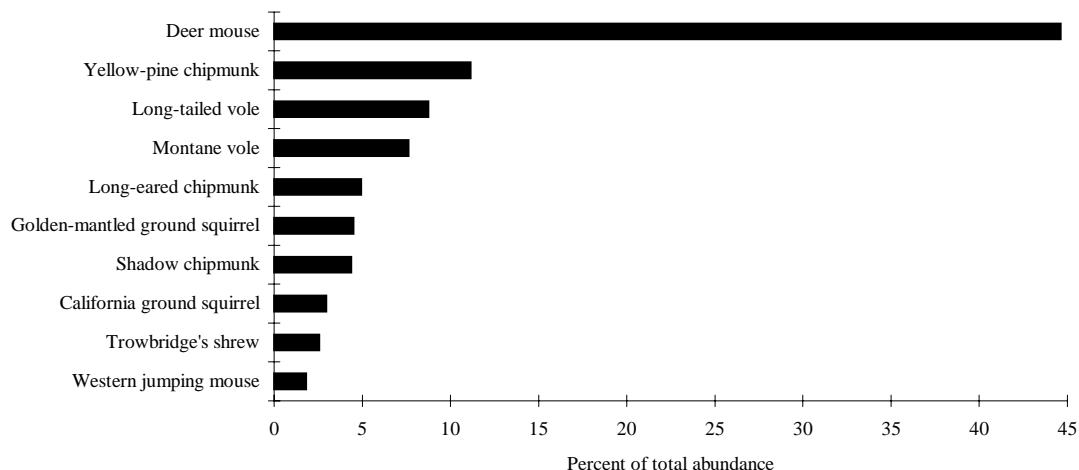


FIG. 33. Ten most abundant mammal species and their contribution to total mammal abundance.

### ***Regression Model for Small Mammal Abundance***

Small mammal abundance with deer mouse was significantly correlated with only one environmental variable: small mammal abundance increased with increases in aspen–cottonwood ( $r = 0.263$ ,  $P = 0.018$ ). Regression of small mammal abundance on abiotic environmental variables resulted in a 2-variable model: a positive association with south aspects, and a negative association with north aspects ( $\text{adj. } R^2 = 0.069$ ) (Table 76). Regression on channel variables resulted in no variables being selected. Regression on vegetation variables resulted in a 2-

variable model: positive association with large logs and negative association with small logs (adj.  $R^2 = 0.053$ ). Backwards step-wise regression on these 4 key variables resulted in a weak one-variable model, where small mammal abundance increased in association with south aspects (adj.  $R^2 = 0.046$ ,  $B = 7.364$ , SE of  $B = 3.368$ , Beta = 0.240,  $T = 2.187$ ,  $P = 0.032$ ) (Table 76).

TABLE 76. Variables selected in step-wise regressions between 3 groups of environmental variables ( $n = 22$ ) and mammal species abundance. N = negative association and P = positive association at  $P \leq 0.10$ . Bolded = selected in the final regression at  $P \leq 0.05$  on key variables from each group of environmental variables. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Small mammal abundance	
	With deer mouse	Without deer mouse
<i>Abiotic environment:</i>		
Precipitation	-	N
South aspect	<b>P</b>	-
North aspect	N	-
<i>Vegetation characteristics:</i>		
Meadow	-	<b>P</b>
Small log	N	-
Large log	P	-
Small snag	-	<b>N</b>
<i>Variables in final model</i>	<i>1</i>	<i>3</i>
<i>adj. <math>R^2</math></i>	<i>0.046</i>	<i>0.134</i>

Small mammal abundance with deer mouse removed was correlated ( $P \leq 0.10$ ) with 5 variables: a positive correlation with meadow ( $r = 0.290$ ,  $P = 0.009$ ), and negative correlation with precipitation ( $r = -0.242$ ,  $P = 0.031$ ), small logs ( $r = -0.260$ ,  $P = 0.020$ ), small snags ( $r = -0.278$ ,  $P = 0.013$ ), and large snags ( $r = -0.284$ ,  $P = 0.011$ ). The regression models were also stronger than total abundance models (Table 76). Regression of small mammal abundance on abiotic environmental variables resulted in a one-variable model: a negative association with precipitation (adj.  $R^2 = 0.069$ ). Regression on channel variables resulted in no variables being selected. Regression on vegetation variables resulted in a 2-variable model: a positive association with meadow and a negative association with small snags (adj.  $R^2 = 0.103$ ). Backwards step-wise regression on these 3 key variables resulted in all 3 variables being selected, showing that small mammal abundance without deer mouse increased with increases in meadow and decreases in precipitation and small snags (adj.  $R^2 = 0.134$ ;  $v = 3$ , 76; SS = 269.30, 1340.92; MS = 89.77, 17.64;  $F = 5.09$ ,  $P = 0.003$ ) (Tables 76 and 77). This model appeared to be more indicative of small mammal abundance, and therefore small mammal abundance with deer mouse removed was used for all future analyses of mammal abundance.

TABLE 77. Final regression model of key environmental variables related to small mammal abundance (without deer mouse). Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
Small snags	-0.437	0.221	-0.216	-1.979	0.051
Precipitation	-2.773	1.425	-0.206	-1.946	0.055
Meadow	2.928	1.631	0.198	1.795	0.077

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with precipitation in the basin ( $r = -0.353$ ,  $P = 0.001$ ). It is possible that the positive relationship observed between small mammal abundance and precipitation is a consequence of disturbance being higher in areas with lower precipitation. An analysis of covariance with precipitation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was potentially responsible for the observed relationship between small mammal abundance and precipitation (Table 78). However, the results of this analysis could simply be reflecting the marginal relationship between precipitation and small mammal abundance.

I looked for potential thresholds in mammal abundance in relation to the 3 primary environmental variables associated with variation in abundance (small snags, precipitation, and meadow). No potential thresholds were observed.

TABLE 78. Analysis of covariance exploring the relationship between small mammal abundance and elevation with disturbance as a covariate. SS = sum of squares.  $v$  = degrees of freedom. MS = mean square.

Source of variation	SS	$v$	MS	F	P
Within + residual	1271.39	75	16.95		
Regression	217.75	1	217.75	12.85	0.001
Precipitation	79.59	3	26.53	1.57	0.205
Model	338.84	4	84.71	5.00	0.001
Total	1610.22	79	20.38		

#### *Small Mammal Abundance by Basin Orientation*

No difference in small mammal abundance (without deer mouse) was observed in relation to basin orientation (ANOVA,  $P = 0.424$ ).

#### *Gradients of Small Mammal Abundance*

Of the 28 species captured during Sherman trap sampling, only 10 species and an additional 2 genera had a frequency of occurrence high enough ( $\geq 10\%$ ) to be entered into the PCA. Two genera (*Mustela* and *Sorex*) were used in lieu of individual species because in each case, one or more of the congeners had a frequency of occurrence  $\geq 10\%$ , and some individuals captured could not be identified to species. Species were pooled together such that the analysis would reflect all species in the genus.

Six factors had eigen values  $\geq 1.0$  and together explained 63.9 % of the variation in small mammal abundance among reaches (Table 79). Factor 1 accounted for 15.4% of the variation, and was positively associated with deer mouse, and negatively associated with montane vole and shrews. Correlations between factor scores and environmental variables showed that factor 1

represented a gradient of meadow to forest. Other environmental variables correlated with factor 1 included positive correlations with gradient, precipitation, and log density.

Factor 2 accounted for 13.7% of the variation, and was positively associated with yellow-pine chipmunk and golden-mantled ground squirrel (*Spermophilus lateralis*), 2 of the most abundant rodents in the sample, surpassed in abundance by only the deer mouse and long-tailed vole (Table 79). These species were apparently more abundant in dry environments, indicated by the negative correlation of the factor with precipitation, and positive correlation with drier aspects (north and east).

Factor 3 accounted for 10.4% of the variation, and had a positive association with long-eared chipmunk (*Tamias quadrimaculatus*), California ground squirrel (*Spermophilus beecheyi*), and Douglas squirrel (Table 79). These were the largest-bodied rodents in the sample, and they appear to be associated with moist, low-elevation, forested areas. This factor was negatively correlated with distance to the mouth, elevation, meadow, and subalpine conifer, and positively correlated with alder–willow and mixed conifer.

Factor 4 accounted for 9.6% of the variation and was positively associated with long-tailed vole, and negatively associated with shadow chipmunk (*Tamias senex*) (Table 79). The long-tailed vole is the second most abundant rodent in the sample. Long-tailed voles were correlated with alder–willow, and negatively correlated with mixed conifer vegetation. Factor 4 was also negatively correlated channel gradient and canopy cover index, and positively correlated with distance from mouth, elevation, and width. These species appear to be more abundant in association with large streams with well-developed alder–willow vegetation in higher elevation areas.

Factors 5 and 6 together accounted for a small proportion of the variation (<15%) explained by the PCA and were not indicative of gradients (Table 79). Factor 5 accounted for 8.0% of the variation among reaches and was associated with northern flying squirrel (*Glaucomys sabrinus*), Western jumping mouse (*Zapus princeps*), and weasels, and negatively associated with lodgepole chipmunk (*Tamias speciosus*). Factor 6 accounted for 6.8% of the variation among reaches and was associated with mountain pocket gopher (*Thomomys monticola*). It was positively correlated with alder–willow and aspen–cottonwood. In summary, the gradients in community composition were characterized by gradients in habitat association from meadow to forest, east side versus west side environmental conditions, low elevation versus high elevation forests, and the abundance of riparian woodland vegetation (i.e., alder–willow and aspen–cottonwood vegetation).

#### ***Small Mammal Abundance Gradients in Relation to Environment Gradients***

Several relationships existed between small mammal abundance gradients and environmental gradients (Table 80). All factors other than factor 5 (riparian associates) were correlated with one or more environmental factors. Small mammal factors 1, 3, and 4 were correlated with the forest to meadow gradient, indicating that deer mouse and long-tailed vole were more abundant in areas with higher elevation and higher precipitation, and montane vole (*Microtus montanus*), shrews, California ground squirrel, Douglas squirrel, long-eared chipmunk, and shadow chipmunk were more abundant in areas with lower elevation and lower precipitation.

Mammal factor 4 showed the strongest relationship with the channel flow gradient, indicating that long-tailed vole was more abundant and long-eared chipmunk was less abundant in areas with high channel flow characteristics. The greatest breadth of relationships between small mammal abundance and environmental gradients were observed in relation to the forest to meadow gradient. Deer mouse, California ground squirrel, Douglas squirrel, long-eared chipmunk, shadow chipmunk were all more abundant in forest environments, whereas montane vole, shrews, long-tailed vole, and mountain pocket gopher were all more abundant in meadow environments. The abundance of mountain pocket gopher was the sole correlate with alder–willow and aspen–cottonwood gradients. The remaining gradients had minor relationships with small mammal abundance.



TABLE 79. Principal components analysis of small mammal community composition and abundance based on Sherman trap data gathered at sample reaches ( $n = 80$ ) in the Lake Tahoe basin. Bolded values indicate variables most associated with each factor.

Species	Scientific Name	Factor 1 Score	Factor 2 Score	Factor 3 Score	Factor 4 Score	Factor 5 Score	Factor 6 Score
Deer mouse	<i>Peromyscus maniculatus</i>	<b>0.625</b>	0.276	-0.085	-0.001	0.184	0.280
Montane vole*	<i>Microtus montanus</i>	<b>-0.799</b>	0.123	-0.160	0.271	-0.098	0.122
Shrews*	<i>Sorex</i> sp.†	<b>-0.687</b>	-0.180	0.120	-0.240	0.206	0.282
Yellow-pine chipmunk*	<i>Tamias amoenus</i>	0.016	<b>0.820</b>	-0.058	0.059	0.066	0.137
Golden mantled ground squirrel	<i>Spermophilus lateralis</i>	0.082	<b>0.755</b>	0.168	-0.093	-0.145	-0.212
California ground squirrel	<i>Spermophilus beecheyi</i>	0.036	0.134	<b>0.829</b>	0.202	-0.020	0.023
Long-eared chipmunk*	<i>Tamias quadrimaculatus</i>	0.149	0.314	<b>0.664</b>	-0.303	0.041	-0.186
Douglas' squirrel*	<i>Tamiasciurus douglasii</i>	-0.145	-0.204	<b>0.598</b>	-0.133	-0.043	-0.017
Long-tailed vole*	<i>Microtus longicaudus</i>	0.070	0.055	0.121	<b>0.712</b>	0.000	0.405
Shadow chipmunk*	<i>Tamias senex</i>	0.116	0.114	0.088	<b>-0.726</b>	0.061	0.151
Northern flying squirrel	<i>Glaucomys sabrinus</i>	0.032	0.197	-0.128	-0.140	<b>0.737</b>	-0.263
Western jumping mouse	<i>Zapus princeps</i>	0.210	-0.302	0.025	0.116	<b>0.601</b>	0.253
Lodgepole chipmunk*	<i>Tamias speciosus</i>	0.350	0.225	-0.257	0.070	<b>-0.527</b>	0.064
Weasels	<i>Mustela</i> sp.††	0.095	0.205	-0.228	0.393	<b>0.400</b>	0.148
Mountain pocket gopher*	<i>Thomomys monticola</i>	-0.087	-0.022	-0.071	0.024	-0.075	<b>0.853</b>

\* Data were log transformed ( $\ln(x+1)$ ) before analysis.

† Shrew species included *Sorex monticolus*, *S. trowbridgii*, and *S. vagrans*

†† Weasel species included *Mustela frenata* and *M. erminea*.

TABLE 80. Significant ( $P \leq 0.10$ ) correlations between small mammal abundance gradients and environmental gradients, as defined by principal components analysis (PCA). Bolded values indicate  $P \leq 0.05$ . N and P indicate non-significant (n.s.) negative and positive correlations, respectively.

Environmental gradient	Small mammal abundance gradient*											
	Factor 1		Factor 2		Factor 3		Factor 4		Factor 5		Factor 6	
	r	P	r	P	r	P	r	P	r	P	r	P
<i>Physical gradient:</i>												
1. Elevation–precipitation	<b>0.363</b>	<b>0.001</b>	N	n.s.	<b>-0.385</b>	<b>&lt;0.001</b>	<b>0.267</b>	<b>0.017</b>	N	n.s.	N	n.s.
2. Channel flow	N	n.s.	-0.205	0.068	N	n.s.	<b>0.258</b>	<b>0.021</b>	N	n.s.	P	n.s.
<i>Vegetation gradient:</i>												
1. Forest to meadow	<b>-0.277</b>	<b>0.013</b>	N	n.s.	<b>-0.325</b>	<b>0.003</b>	<b>0.261</b>	<b>0.019</b>	P	n.s.	0.187	0.097
2. Subalpine vegetation	P	n.s.	P	n.s.	<b>-0.257</b>	<b>0.021</b>	P	n.s.	N	n.s.	P	n.s.
3. Alder–willow	P	n.s.	N	n.s.	P	n.s.	P	n.s.	P	n.s.	<b>0.229</b>	<b>0.041</b>
4. Aspen–cottonwood	N	n.s.	P	n.s.	P	n.s.	N	n.s.	N	n.s.	<b>0.316</b>	<b>0.004</b>
<i>Woody debris gradient:</i>												
1. Snag and log	<b>0.403</b>	<b>&lt;0.001</b>	N	n.s.	N	n.s.	N	n.s.	N	n.s.	N	n.s.

\* Factor 1 = Montane vole and shrews to deer mouse; Factor 2 = Yellow-pine chipmunk and golden-mantled ground squirrel; Factor 3 = California ground squirrel, Douglas squirrel, long-eared chipmunk; Factor 4 = Long-tailed vole and shadow chipmunk; Factor 5 = Riparian associates; Factor 6 = Pocket gopher

## *Patterns of Mammal Alpha Diversity by Habitat Association*

### **General Patterns**

Patterns of mammal richness were explored in relation to association with 2 major habitat conditions: aquatic–riparian–meadow versus upland. Upland-associated species were observed on every reach, whereas aquatic–riparian–meadow-associated species were lacking on a small proportion of reaches (Table 81).

The contribution of individual species to the richness values for each group varied based on the relative frequency of the species. Aquatic–riparian–meadow-associated species exhibited a steep 60% change in frequency of occurrence across the 5 most frequent species, and then a relatively gradual shift across the remaining species (Fig. 34). The upland associates exhibited a gradual shift in frequency of occurrence from 100% to 25% frequency of occurrence across the 10 most frequent upland species (Fig. 35).

TABLE 81. Descriptive statistics for the richness of 2 mammal groups based on habitat associations. Data were collected at sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Habitat groups	Total species possible	Freq. (%)	Min.	Max.	Ave.	SE
Aquatic–riparian–meadow-associated species	12	88	0	6	2.1	0.15
Upland-associated species	23	100	2	12	6.6	0.25

### **Environmental Relationships of Mammal Groups**

#### *Correlations*

Aquatic–riparian–meadow associates and upland associates had significant correlations with numerous environmental variables, with most correlations being opposite for the two species groups (Table 82). Five variables shifted from negative to positive correlations from aquatic–riparian–meadow associates to upland associates: channel gradient, mixed conifer, canopy cover index, large logs and large snags. Two variables shifted from negative to positive correlations from aquatic–riparian–meadow associates to upland associates: channel width and meadow. The aquatic–riparian–meadow and upland species groups were both positively correlated with elevation, aspen–cottonwood and small logs. Both species groups were negatively correlated with small snags.

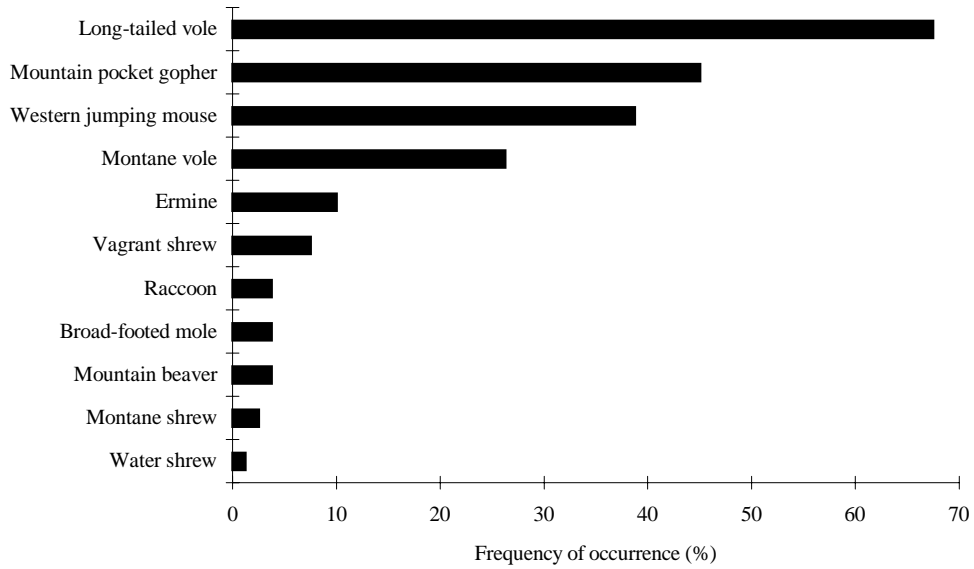


FIG. 34. Aquatic-riparian-meadow-associated mammal species and their frequency of occurrence ( $n = 80$  sample reaches) in the Lake Tahoe basin, 1995 to 1996.

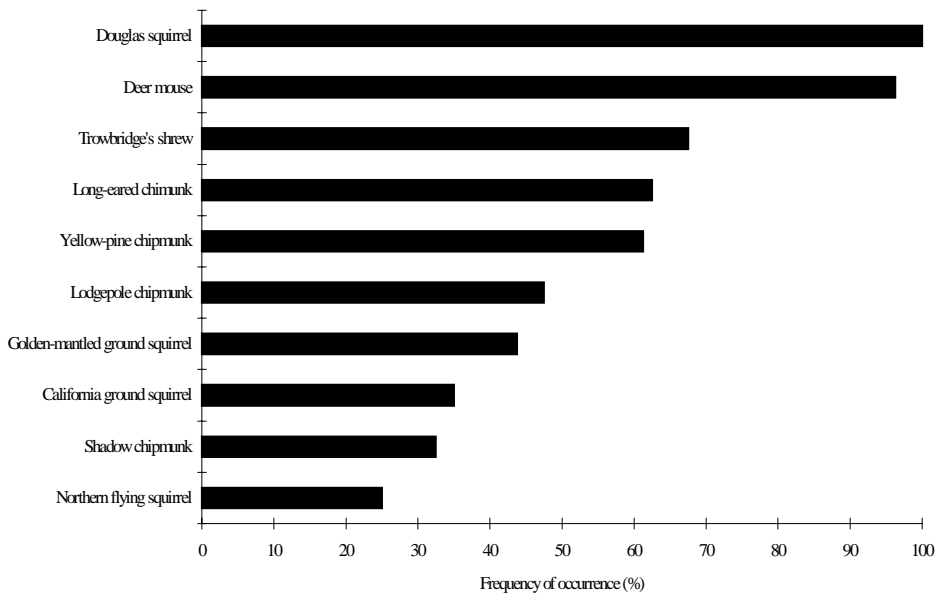


FIG. 35. Ten most frequent upland-associated mammal species and their frequency of occurrence ( $n = 80$  sample reaches) in the Lake Tahoe basin, 1995 to 1996.

TABLE 82. Significant correlations ( $P \leq 0.10$ ) between species richness for 2 mammal groups and 22 environmental variables. Bolded values indicate  $P \leq 0.05$ . N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Mammal habitat group			
	Aquatic–riparian–meadow-associated species		Upland-associated species	
	r	P	r	P
<i>Abiotic environment:</i>				
Elevation	<b>0.278</b>	<b>0.013</b>	<b>0.280</b>	<b>0.012</b>
<i>Channel characteristics:</i>				
Gradient	-0.196	0.082	<b>0.255</b>	<b>0.022</b>
Width	P	n.s.	-0.203	0.071
<i>Vegetation characteristics:</i>				
Mixed conifer	<b>-0.386</b>	<b>0.005</b>	P	n.s.
Aspen–cottonwood	0.217	0.053	<b>0.232</b>	<b>0.039</b>
Meadow	<b>0.311</b>	<b>0.005</b>	<b>-0.305</b>	<b>0.006</b>
Canopy cover index	<b>-0.334</b>	<b>0.002</b>	<b>0.251</b>	<b>0.025</b>
Small log	P	n.s.	<b>0.301</b>	<b>0.007</b>
Large log	N	n.s.	<b>0.223</b>	<b>0.047</b>
Small snag	<b>-0.261</b>	<b>0.020</b>	N	n.s.
Large snag	<b>-0.231</b>	<b>0.040</b>	P	n.s.

*Regression Model for Aquatic–riparian–meadow-associated Mammal Richness*

Regression of aquatic–riparian–meadow-associate richness on abiotic environmental variables resulted in a one-variable model: positive association with elevation (adj.  $R^2 = 0.065$ ) (Table 83). Regression on channel variables resulted in a one-variable model: a negative association with channel gradient (adj.  $R^2 = 0.026$ ). Regression on vegetation variables resulted in a 3-variable model: a positive association with aspen–cottonwood, and negative associations with mixed conifer and canopy cover index (adj.  $R^2 = 0.069$ ). Backwards step-wise regression on these 5 key variables resulted in a weak 3-variable vegetation model, where aquatic–riparian–meadow-associated species richness increased with increases in aspen–cottonwood and decreases in mixed conifer and canopy cover index (adj.  $R^2 = 0.215$ ) (Tables 83 and 84).

TABLE 83. Variables selected in step-wise regressions between 3 groups of environmental variables ( $n = 22$ ) and species richness for 2 mammal groups. N = negative association and P = positive association at  $P \leq 0.10$ . Bolded = selected in the final regression at  $P \leq 0.05$  on key variables from each group of variables. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Mammal habitat group	
	Aquatic–riparian– meadow-associated species	Upland- associated species
<i>Abiotic environment:</i>		
Elevation	P	<b>P</b>
<i>Channel characteristics:</i>		
Gradient	N	P
<i>Vegetation characteristics:</i>		
Mixed conifer	<b>N</b>	-
Aspen–cottonwood	<b>P</b>	<b>P</b>
Meadow	-	<b>N</b>
Canopy cover index	<b>N</b>	-
<i>Variables in final model</i>	3	3
<i>adj. <math>R^2</math></i>	0.215	0.198

TABLE 84. Final linear regression model of key environmental variables in relation to species richness of 2 habitat groups (aquatic–riparian–meadow and upland associates). Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
<i>Aquatic–riparian–meadow associates:</i>					
Mixed conifer	-0.734	0.283	-0.293	-2.594	0.011
Aspen–cottonwood	2.201	0.855	0.258	2.573	0.012
Canopy cover index	-0.011	0.006	-0.226	-1.990	0.050
<i>Upland associates:</i>					
Meadow	-2.304	0.757	-0.309	-3.043	0.003
Aspen–cottonwood	3.937	1.492	0.267	2.638	0.010
Elevation	7.405	2.911	0.257	2.544	0.013

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ( $r = -0.515$ ,  $P < 0.001$ ). It is possible that the positive relationship observed between aquatic–riparian–meadow associate richness and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was not

responsible for the observed relationship between aquatic–riparian–meadow associate richness and elevation (Table 85).

TABLE 85. Analysis of covariance exploring the relationship between aquatic–riparian–meadow-associated mammal richness and elevation with disturbance as a covariate. SS = sum of squares.  $\nu$  = degrees of freedom. MS = mean square.

Source of variation	SS	$\nu$	MS	F	<i>P</i>
Within + residual	120.99	75	1.61		
Regression	0.51	1	0.51	0.31	0.577
Elevation	10.16	3	3.39	2.10	0.107
Model	15.76	4	3.94	2.44	0.054
Total	136.75	79	1.73		

I looked for potential thresholds in aquatic–riparian–meadow-associated mammal species richness in relation to the 3 environmental variables selected in the final regression model. The presence of  $\geq 1\%$  aspen–cottonwood within the reach was consistently associated with the presence of  $\geq 1$  aquatic–riparian–meadow species (Fig. 36), and the richness of aquatic–riparian–meadow mammal species was significantly greater where aspen–cottonwood was present (1-tailed test, pooled variance,  $t = 2.37$ ,  $P = 0.012$ ). In addition, aquatic–riparian–meadow species richness appeared to be lower on reaches with  $> 40\%$  canopy cover index (Fig. 37), and richness of aquatic–riparian–meadow mammal species was significantly greater where canopy over index was  $> 40\%$  (1-tailed test, pooled variance,  $t = 1.43$ ,  $P = 0.088$ ).

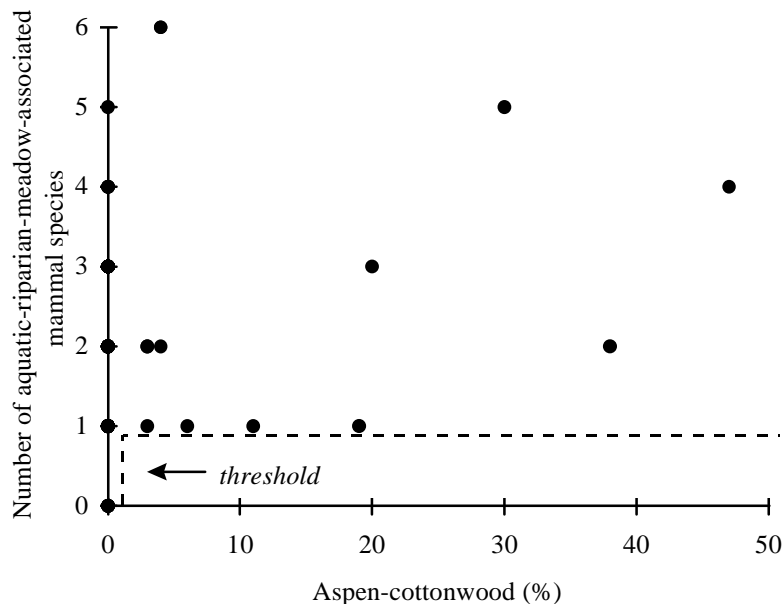


FIG. 36. Threshold between aspen–cottonwood and the richness of aquatic–riparian–meadow-associated mammal species in the Lake Tahoe basin, 1995 to 1996.

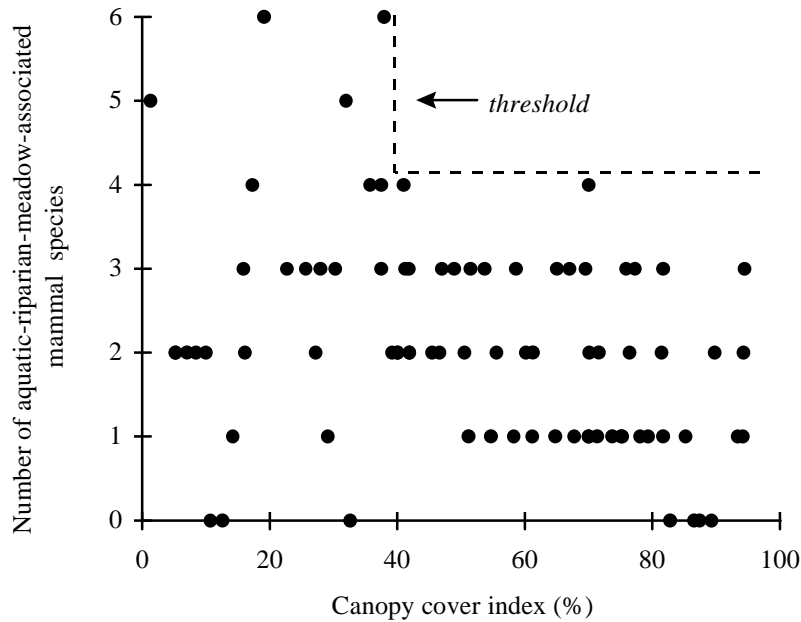


FIG. 37. Threshold between canopy cover index (as measured by a spherical convex densiometer) and the richness of aquatic-riparian-meadow-associated mammal species in the Lake Tahoe basin, 1995 to 1996.

#### *Regression Model for Upland-associated Mammal Richness*

Regression of upland-associated species richness on abiotic environmental variables resulted in a one variable model: a positive association with elevation (adj.  $R^2 = 0.065$ ) (Table 83). Regression on channel variables resulted in a one-variable model: a positive association with channel gradient (adj.  $R^2 = 0.026$ ). Regression on vegetation variables resulted in a 2-variable model: a positive association with aspen-cottonwood, and a negative association with meadow (adj.  $R^2 = 0.141$ ). Backwards step-wise regression on these 4 key variables resulted in a weak 3-variable model, where upland-associated species richness increased with increases in aspen-cottonwood and elevation, and decreases in meadow (adj.  $R^2 = 0.198$ ) (Tables 83 and 84).

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ( $r = -0.515$ ,  $P < 0.001$ ). It is possible that the positive relationship observed between upland-associated species richness and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal-sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible for the observed relationship between upland-associated species richness and elevation, but also that the relationship between upland-associated species richness and elevation is weak (Table 86).

I looked for potential thresholds in upland-associated mammal species richness in relation to the 3 environmental variables selected in the final regression model. The presence of  $\geq 1\%$  aspen-cottonwood within the reach was consistently associated with  $> 5$  upland-associated species (Fig. 38), and upland mammal species richness was significantly greater on reaches with aspen-cottonwood (1-tailed test, pooled variance,  $t = 2.29$ ,  $P = 0.018$ ). In addition, reaches occurring at elevations  $> 2250$  m were consistently associated with  $\geq 5$  upland-associated species (Fig. 39). The richness of upland-associated mammal species was significantly greater on reaches above 2250 m in elevation (1-tailed test, pooled variance,  $t = 2.49$ ,  $P = 0.010$ ).



TABLE 86. Analysis of covariance exploring the relationship between upland-associated mammal species richness and elevation with disturbance as a covariate. SS = sum of squares.  $\nu$  = degrees of freedom. MS = mean square.

Source of variation	SS	$\nu$	MS	F	P
Within + residual	381.44	75	5.09		
Regression	1.71	1	1.71	0.34	0.564
Elevation	26.60	3	8.87	1.74	0.165
Model	27.05	4	6.76	1.33	0.267
Total	408.49	79	5.17		

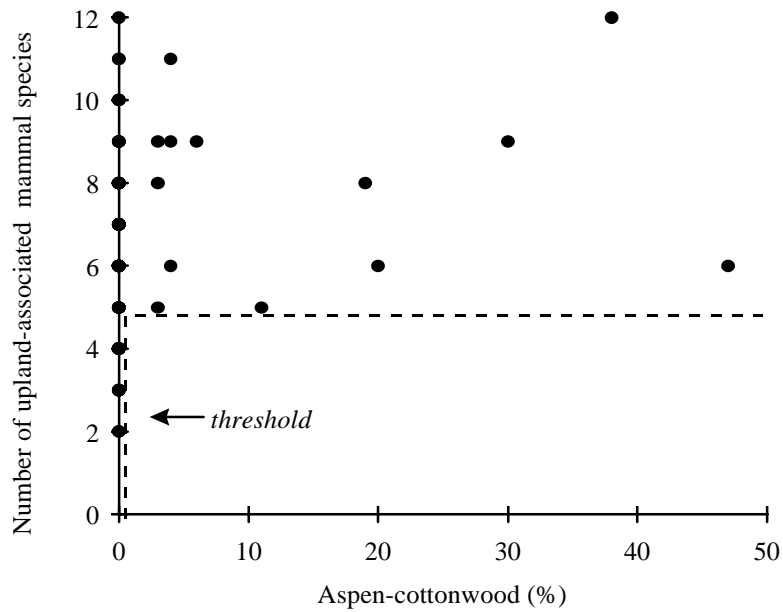


FIG. 38. Threshold relationship between aspen–cottonwood and the richness of upland-associated mammal species in the Lake Tahoe basin, 1995 to 1996.

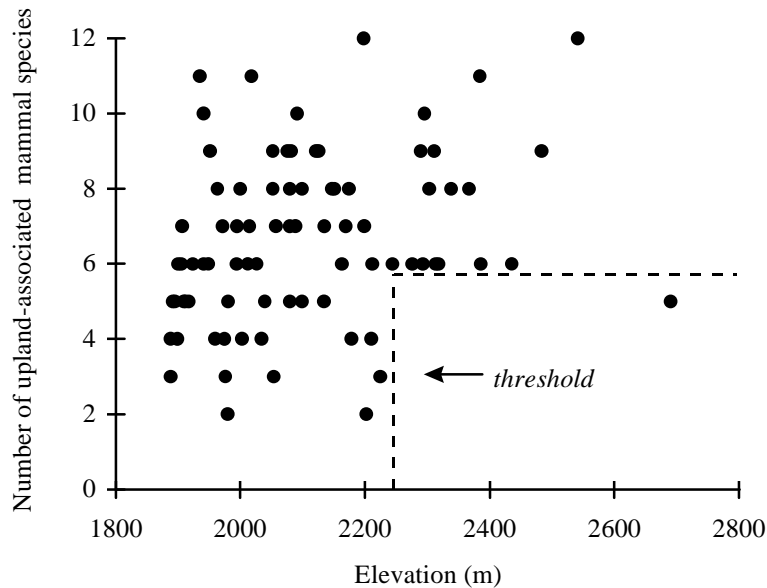


FIG. 39. Threshold relationship between elevation and the richness of upland-associated mammal species in the Lake Tahoe basin, 1995 to 1996.

#### *Mammal Group Richness by Environmental Gradients*

Aquatic–riparian–meadow associate richness was positively correlated with elevation–precipitation and forest to meadow gradients, and negatively correlated with the snag and log gradient (Table 87). Upland-associated species richness was negatively correlated with both channel flow and forest to meadow gradients (Table 87).

#### *Mammal Group Richness by Basin Orientation*

The richness of aquatic–riparian–meadow-associated mammals varied significantly by basin orientation ( $v = 3, 76; SS = 12.75, 123.99; MS = 4.25, 1.63; F = 2.61, P = 0.058$ ). North ( $\bar{x} = 2.4, SE = 0.29$ ) and west ( $\bar{x} = 2.5, SE = 0.23$ ) sides of the basin had higher richness than east ( $\bar{x} = 1.6, SE = 0.33$ ) and south ( $\bar{x} = 1.8, SE = 0.31$ ) sides, but none were significantly different from one another (based on Tukey's test).

The richness of upland-associated mammals varied significantly by basin orientation ( $v = 3, 76; SS = 53.58, 354.91; MS = 17.86, 4.67; F = 3.82, P = 0.013$ ). The east side had greater richness than the south side, with richness being highest in the east, then north, then west, and lowest in the south. The east side had the highest aspen–cottonwood and mixed conifer, and the lowest precipitation and channel width.

TABLE 87. Correlations between mammal habitat group variables and principal component analysis factors. Bolded values indicate significant correlations ( $P \leq 0.10$ ).  $r$  = correlation coefficients. Data were collected at sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Mammal habitat groups			
	Aquatic–riparian– meadow-associated species		Upland-associated species	
	$r$	$P$	$r$	$P$
<i>Physical gradient:</i>				
1. Elevation–precipitation	<b>0.300</b>	<b>0.007</b>	0.158	0.161
2. Channel flow	0.129	0.256	<b>-0.319</b>	<b>0.004</b>
<i>Vegetation gradient:</i>				
1. Forest to meadow	<b>0.408</b>	<b>&lt;0.001</b>	<b>-0.240</b>	<b>0.032</b>
2. Subalpine vegetation	0.110	0.332	-0.017	0.878
3. Alder–willow	0.116	0.307	0.106	0.349
4. Aspen–cottonwood	0.165	0.144	0.144	0.202
<i>Woody debris gradient:</i>				
1. Snag and log	<b>-0.192</b>	<b>0.087</b>	0.173	0.125

#### *Summary of Environmental Relationships of Mammal Groups*

Three environmental variables appeared to vary between the 2 habitat groups (Table 88). The richness of aquatic–riparian–meadow–associates was associated with lower gradient channels, a greater abundance of meadow, and lower canopy cover index compared to upland associates. In contrast, 2 variables were similarly related to the richness of both species groups: elevation and aspen–cottonwood were both positively associated with the richness of each species group.

TABLE 88. Summary of contrasting relationships between the richness of 2 mammal habitat groups (aquatic–riparian–meadow and upland associates) and environmental variables. Data were collected at sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variable sets	Mammal habitat group	
	Aquatic–riparian–meadow w associates	Upland associates
<i>Channel</i>	Gradient	→
<i>Vegetation</i>	← Meadow	→
	Canopy cover index	→

I looked for potential thresholds between the richness of each habitat group and the 5 variables associated with both groups. Aquatic–riparian–meadow species richness appeared to decline as channel gradient increased up to 10%, and then was relatively stable (Fig. 40), and was significantly lower on reaches with  $> 10\%$  channel gradient (1-tailed test, pooled variance,  $t = 1.45$ ,  $P = 0.078$ ).

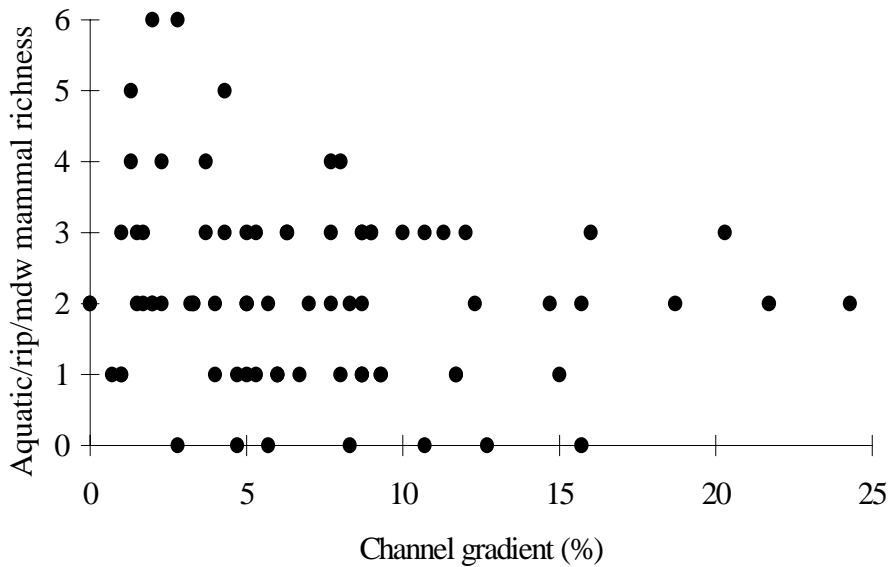


FIG. 40. Threshold relationship between channel gradient (%) and the richness of aquatic–riparian–meadow-associated mammal species in the Lake Tahoe basin.

### *Patterns of Rarity*

#### *General Patterns*

The distribution of relative frequencies of species showed that 25 mammal species (approximately 70%) were present on less than 25% of the reaches (Fig. 41), and a total of 16 species were present on less than 10% of the reaches. Each rare species occurred on an average 4.5 reaches ( $SE = 0.92$ ), and at least one rare species was present on 62.5% ( $n = 50$ ) of the reaches (Table 89). Alternatively, each common species occurred on an the average of 43.7 reaches ( $SE = 4.84$ ), and at least one common species was observed on every reach (Table 89). Correlations between the number of rare and common species per reach was low and not significant ( $r = 0.166$ ,  $P = 0.140$ ).

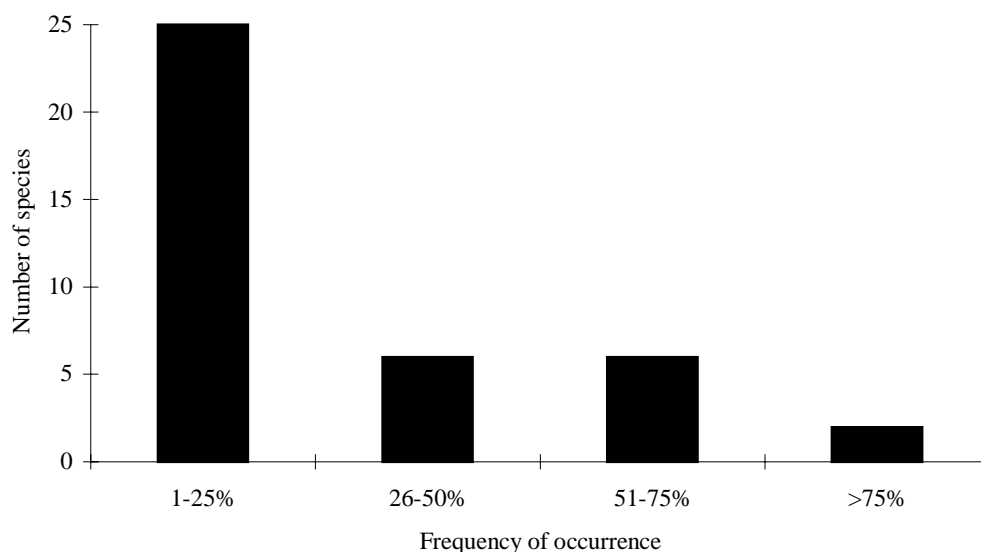


FIG. 41. Frequency of occurrence of mammal species detected on 80 stream reaches in the Lake Tahoe basin, 1995 to 1996.

TABLE 89. Descriptive statistics for measures of frequency for mammal occurrence. Species considered rare if frequency of occurrence  $< 10\%$ , common if  $\geq 10\%$ . Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin.

Frequency variable	Minimum	Maximum	Average	SE
Number of rare species	0	7	1.2	0.16
Number of common species	2	13	7.5	0.26
Percent rare species	0	50.0	12.8	1.44
Percent common species	50.0	100.0	87.2	1.44

I also calculated the proportion of the mammal assemblage comprised by each frequency class. The proportion of rare species averaged 12.8 %, whereas the proportion of common species averaged 87.2% per reach (Table 89).

Significant correlations were observed among the 4 measures of rarity (Table 90). The high correlations between number of rare species and the percent of both rare and common species, indicated that the most informative patterns of association could be discerned by analyzing the number of rare versus common species.

TABLE 90. Significant ( $P \leq 0.10$ ) correlations among mammal frequency variables. Bolded values indicate  $P \leq 0.05$ . Shading indicates redundant cells. Data were collected at sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Frequency variable	Number of rare species		Number of common species		Percent rare species	
	r	P	r	P	r	P
Number of rare species						
Number of common species	0.166	0.140				
Percent rare species	<b>0.881</b>	<b>&lt;0.001</b>	-0.140	0.217		
Percent common species	<b>-0.881</b>	<b>&lt;0.001</b>	0.140	0.217	<b>-1.000</b>	<b>&lt;0.001</b>

### *Environmental Relationships of Mammal Rarity*

#### *Correlations*

The number of rare species showed few significant correlations with physical and vegetation characteristics compared to the number of common species (Table 91). One variable was significantly correlated with the number of rare species, aspen–cottonwood, a rare vegetation type ( $r = 0.400$ ,  $P < 0.01$ ). Conversely, the number of common species was significantly correlated with 6 environmental variables: positive correlations with elevation, channel gradient, and small logs; and negative correlations with channel sinuosity and width.

TABLE 91. Significant ( $P \leq 0.10$ ) correlations between mammal frequency variables and environmental gradients, as defined by principal components analysis. Bolded values indicate  $P \leq 0.05$ . N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental variables	Mammal frequency variables			
	Number of rare species		Number of common species	
	r	P	r	P
<i>Abiotic environment:</i>				
Elevation	P	n.s.	<b>0.396</b>	<b>&lt;0.001</b>
<i>Channel characteristics:</i>				
Gradient	N	n.s.	<b>0.284</b>	<b>0.011</b>
Width	N	n.s.	<b>-0.230</b>	<b>0.040</b>
Sinuosity	P	n.s.	<b>-0.251</b>	<b>0.025</b>
<i>Vegetation characteristics:</i>				
Aspen–cottonwood	<b>0.400</b>	<b>&lt;0.001</b>	P	n.s.
Canopy cover index	N	n.s.	-0.209	0.062
Small logs	P	n.s.	<b>0.285</b>	<b>0.010</b>

### *Regression Model for Rare Mammal Richness*

The number of rare species was compared to environmental variables using multiple regression (Table 92). Regression analyses for abiotic environment and channel variables resulted in no variables being selected for either model. The regression model for vegetation variables consisted of 3 variables: positive associations with aspen–cottonwood and lodgepole pine, and negative associations with small snags. (adj.  $R^2 = 0.209$ ). The final backwards regression run with the 3 vegetation variables resulted in a 2-variable model: aspen–cottonwood and lodgepole pine (adj.  $R^2 = 0.189$ ) (Tables 92 and 93).

TABLE 92. Variables selected in step-wise regressions between 3 groups of environmental variables ( $n = 22$ ) and the number of species in each of 2 frequency classes. N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Bolded = selected in the final regression at  $P \leq 0.05$  on key variables from each group of environmental variables. Data were collected at 80 sample reaches in the Lake Tahoe basin, 1995 to 1996.

Environmental variable	Mammal frequency variable	
	Number of rare species	Number of common species
<i>Abiotic environment:</i>		
Elevation	-	<b>P</b>
<i>Channel character:</i>		
Gradient	-	P
<i>Vegetation character:</i>		
Aspen–cottonwood	<b>P</b>	-
Lodgepole pine	<b>P</b>	-
Small snag	N	<b>N</b>
Small log	-	<b>P</b>
Canopy cover index	-	<b>P</b>
<i>Variables in final model</i>	2	4
<i>adj. <math>R^2</math></i>	0.189	0.245

TABLE 93. Final backwards regression model of key environmental variables related to mammal frequency variables. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	P
<i>Number of rare mammals:</i>					
Aspen-cottonwood	4.971	0.943	0.431	4.211	<0.001
Lodgepole pine	1.042	0.477	0.224	2.186	0.032
<i>Number of common mammals:</i>					
Elevation	0.020	3.071	0.311	2.937	0.004
Canopy cover index	0.023	0.009	0.266	2.582	0.012
Small logs	0.369	0.148	0.290	2.494	0.015
Small snags	-0.251	0.124	-0.244	-2.030	0.046

#### *Regression Model for Common Mammal Richness*

Individual regression models for the number of common mammal species compared to each of the 3 environmental variable groups resulted in a 2-variable model for abiotic environment (positive association with elevation, negative association with precipitation; adj.  $R^2 = 0.171$ ), a one-variable model for channel characteristics (a positive association with gradient; adj.  $R^2 = 0.069$ ), and 3-variable model for vegetation characteristics (positive associations with canopy cover index and small logs, and a negative association with small snags; adj.  $R^2 = 0.169$ ) (Table 92). These 5 key variables were entered into a backward stepwise regression, resulting in a 4-variable model, where common mammal richness increased with increases in elevation, canopy cover index, and small logs, and decreases in small snags (adj.  $R^2 = 0.245$ ) (Tables 92 and 93).

Meso-scale disturbance (measured as the proportion of the area within 250 m of the center of the reach that is physically disturbed) was negatively correlated with elevation in the basin ( $r = -0.515$ ,  $P < 0.001$ ). It is possible that the negative relationship observed between the number of common mammals and elevation is a consequence of disturbance being higher in areas with lower elevation. An analysis of covariance with elevation partitioned into 4 equal sized groups, and meso-scale disturbance as the covariate showed that disturbance was not responsible the observed relationship between rare mammal richness and elevation (adj.  $R^2 = 0.071$ ) (Table 94).



TABLE 94. Analysis of covariance exploring the relationship between the number of rare mammal species and elevation with disturbance as a covariate. SS = sum of squares.  $\nu$  = degrees of freedom. MS = mean square.

Source of variation	SS	$\nu$	MS	F	P
Within + residual	366.87	75	4.89		
Regression	2.43	1	2.43	0.50	0.483
Elevation	45.46	3	15.15	3.10	0.032
Model	48.93	4	12.23	2.50	0.049
Total	415.80	79	5.26		

#### *Mammal Rarity and Environmental Gradients*

The number of common species was positively correlated with elevation–precipitation (physical factor 1) and negatively correlated with channel flow (physical factor 2) (Table 95). The number of rare species did not have significant correlations with either physical gradient. The number of rare species was positively correlated with forest to meadow (vegetation factor 1) and aspen–cottonwood (vegetation factor 4) (Table 95). No correlations were observed between mammal frequency variables and the snag and log gradient (Table 95).

TABLE 95. Significant ( $P \leq 0.10$ ) correlations between mammal frequency variables and environmental gradients (as defined by principal components analysis). Bolded values indicate  $P \leq 0.05$ . N and P indicate non-significant (n.s.) negative and positive correlations, respectively. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Environmental gradient	Number of rare species		Number of common species	
	r	P	r	P
<i>Physical gradient:</i>				
1. Elevation–precipitation	P	n.s.	<b>0.259</b>	<b>0.020</b>
2. Channel flow	P	n.s.	<b>-0.384</b>	<b>&lt;0.001</b>
<i>Vegetation gradient:</i>				
1. Forest to meadow	0.206	0.067	N	n.s.
2. Subalpine vegetation	N	n.s.	P	n.s.
3. Alder–willow	P	n.s.	P	n.s.
4. Aspen–cottonwood	<b>0.266</b>	<b>0.017</b>	P	n.s.
<i>Woody debris gradient:</i>				
1. Snag and log	N	n.s.	P	n.s.

#### *Mammal Rarity by Basin Orientation*

The number of common mammal species was different among basin orientations (ANOVA,  $\nu = 3, 76$ ; SS = 76.08, 339.72; MS = 25.36, 4.47; F = 5.67;  $P = 0.007$ ). It was highest on the north side, and was significantly less on the south side than all the other orientations. The number of rare species did not differ among orientations (ANOVA,  $P = 0.505$ ).

## *Patterns of Beta Diversity*

### *Mammal Species Turnover along Environmental Gradients*

#### *Species Turnover*

The lower of the gains and losses between any two segments represented the beta diversity for the 2 segments—the change in composition that was independent from alpha diversity. The sum of beta diversity across all 3 segment comparisons, “total turnover”, was used as the primary indication of the contribution of a gradient to beta diversity (Table 96). The alder–willow gradient had the highest total turnover ( $n = 12$ ), followed by 2 gradients with a total turnover of 11: elevation and elevation–precipitation. The next 4 gradients had a total turnover of 9: channel flow, forest to meadow, subalpine vegetation, and snags and logs. The remaining 3 gradients had total turnovers of 7 or 8.

Patterns of turnover along each gradient provide additional insights as to their contributions to beta diversity (Table 96). For the elevation gradient, total richness declined from low to high segments, and turnover was highest at the upper end of the gradient. Total richness also declined from low to high segments along the precipitation gradient, with turnover being lower at the upper end of the gradient. The elevation–precipitation gradient showed virtually no change in richness between segments, and turnover was only slightly higher at mid gradient. Total richness and turnover declined from low to high channel flow, as well as from low to high forest to meadow. Along the subalpine vegetation gradient, total richness and turnover were slightly higher mid gradient. The alder–willow gradient showed declines in richness and turnover from low to high segments. Total richness was highest at the upper end of the aspen–cottonwood gradient, but turnover was lightly higher in mid gradient. No changes in total richness and turnover were observed between the lower segments of the snag and log gradient, but richness and turnover did decline between the upper-most segments.

#### *Whittaker's Index of Beta Diversity*

The gradients were evaluated for their relative contribution to beta diversity in part based on a modified Whittaker's beta diversity index ( $\beta_{wMIN}$ ), with the unmodified index value provided for comparison (Table 96). The average  $\beta_{wMIN}$  for segment comparisons along each gradient varied from a low of 0.084 for the precipitation gradient to a high of 0.146 for alder–willow. Next to alder–willow, elevation and channel flow had the next highest values for the beta diversity index. The next 3 gradients were close in value: forest to meadow, subalpine vegetation, and snag and log. Precipitation had much lower  $\beta_{wMIN}$  values.

TABLE 96. Beta diversity index values for mammals within and among 10 environmental gradients. The number of species per segment, the number of species only occurring at upper (“gains”) or lower (“losses”) ends of the gradient, and Whittaker’s (1972) beta diversity index ( $\beta_w$ ) are displayed. A modified version of Whittaker’s beta diversity index ( $\beta_{wMIN}$ ) is also displayed. Bolded values indicate turnover. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	$\beta_w^*$	$\beta_{wMIN}^\dagger$
<i>Elevation:</i>							
seg1:seg2	25	26	28	3	<b>2</b>	0.098	0.077
seg2:seg3	26	27	31	5	<b>4</b>	0.170	0.148
seg3:seg4	27	25	32	<b>5</b>	7	0.231	0.185
<i>Average</i>							<i>0.134</i>
<i>low:high</i>	28	32	35	7	<b>3</b>	<i>0.176</i>	<i>0.094</i>
<i>Precipitation:</i>							
seg1:seg2	30	26	33	<b>3</b>	7	0.179	0.100
seg2:seg3	26	24	29	<b>3</b>	5	0.160	0.115
seg3:seg4	24	27	28	4	<b>1</b>	0.098	0.037
<i>Average</i>							<i>0.084</i>
<i>low:high</i>	33	28	35	<b>2</b>	7	<i>0.148</i>	<i>0.061</i>
<i>Elevation–precipitation:</i>							
seg1:seg2	26	25	30	4	<b>5</b>	0.176	0.154
seg2:seg3	25	27	30	5	<b>3</b>	0.154	0.111
seg3:seg4	27	25	31	<b>4</b>	6	0.154	0.111
<i>Average</i>							<i>0.125</i>
<i>low:high</i>	<i>30</i>	<i>31</i>	<i>35</i>	<i>5</i>	<b>4</b>	<i>0.167</i>	<i>0.167</i>
<i>Channel flow:</i>							
seg1:seg2	29	27	33	<b>4</b>	6	0.179	0.138
seg2:seg3	27	23	31	<b>4</b>	8	0.240	0.148
seg3:seg4	23	24	26	3	<b>2</b>	0.106	0.083
<i>Average</i>							<i>0.123</i>
<i>low:high</i>	33	26	35	<b>2</b>	9	<i>0.186</i>	<i>0.061</i>
<i>Forest to meadow:</i>							
seg1:seg2	26	27	31	5	<b>4</b>	0.170	0.148
seg2:seg3	27	24	30	<b>3</b>	6	0.176	0.111
seg3:seg4	24	27	29	5	<b>2</b>	0.137	0.074
<i>Average</i>							<i>0.111</i>
<i>low:high</i>	<i>31</i>	<i>29</i>	<i>35</i>	<b>4</b>	6	<i>0.167</i>	<i>0.129</i>

TABLE 96 cont.

Gradient	Richness of lower segment	Richness of higher segment	Total richness	Gains	Losses	$\beta_w^*$	$\beta_{wMIN}^\dagger$
<i>Subalpine vegetation:</i>							
seg1:seg2	28	26	30	<b>2</b>	4	0.111	0.071
seg2:seg3	26	28	32	6	<b>4</b>	0.185	0.143
seg3:seg4	28	23	31	<b>3</b>	8	0.216	0.107
Average							0.107
low:high	30	31	35	5	<b>4</b>	0.148	0.129
<i>Alder–willow:</i>							
seg1:seg2	28	25	33	<b>5</b>	8	0.245	0.179
seg2:seg3	25	27	31	6	<b>4</b>	0.192	0.148
seg3:seg4	27	25	30	<b>3</b>	5	0.154	0.111
Average							0.146
low:high	33	30	35	<b>2</b>	5	0.111	0.061
<i>Aspen–cottonwood:</i>							
seg1:seg2	28	23	30	<b>2</b>	7	0.176	0.071
seg2:seg3	23	22	27	<b>4</b>	5	0.200	0.174
seg3:seg4	22	30	32	10	<b>2</b>	0.231	0.067
Average							0.104
low:high	30	32	35	5	<b>3</b>	0.129	0.094
<i>Snag and log:</i>							
seg1:seg2	27	29	33	6	<b>4</b>	0.170	0.138
seg2:seg3	29	28	33	<b>4</b>	5	0.158	0.138
seg3:seg4	28	24	29	<b>1</b>	5	0.115	0.036
average							0.104
low:high	33	29	35	<b>2</b>	6	0.129	0.061

\* Whittaker's beta diversity index:  $S/\alpha - 1$ , where  $S$  = total species richness, and  $\alpha$  = the average species richness of the two segments being compared.

† Modified Whittaker's beta diversity index:  $(S/s_{\max}) - 1$ , where  $S$  = total species richness, and  $s_{\max}$  = the highest richness of the two segments being compared, resulting in a minimum beta diversity index value.

### Species Presence

Species presence contributions to beta diversity are displayed in Table 97. Species contributing to gains and losses between lower and upper segments of each gradient are indicated, along with species showing additional trends of presence (absent from segment 1 or 4) along the gradient. Species specific associations with gradients also indicate the relevance of the gradient to individual species. Most species had frequencies < 10%. Elevation and precipitation were analyzed separately, as well as their combined representation in the elevation–precipitation gradient. Along the elevation gradient, 2 of the 3 species restricted to the lower end of the gradient occurred on more than one reach. Western gray squirrel (*Sciurus griseus*) and raccoon (*Procyon lotor*) only occurred at lower elevations. Additionally, vagrant shrew (*Sorex vagrans*)

and pinon mouse (*Peromyscus truei*) were absent from the highest elevation segment. Four of the 7 species restricted to upper elevations occurred on more than one reach: mountain beaver (*Aplodontia rufa*), brush mouse (*Peromyscus boylii*), desert woodrat and bushy-tailed woodrat (*Neotoma cinerea*). Brush mouse only occurred in the highest elevation reaches. The greater number of species associated with upper elevation segments reflects the positive relationship between alpha diversity and elevation. Along the precipitation gradient, 1 of the 2 species associated with the upper end of the gradient occurred on more than 1 reach; the brush mouse was restricted to reaches with the highest precipitation. Two additional species were absent from reaches with the lowest precipitation, porcupine (*Erithrozon dorsatum*) and broad-footed mole (*Scapanus latimanus*). Four of the 7 species associated with the lower end of the precipitation gradient were present on more than one reach: montane shrew (*Sorex monticolus*), Western gray squirrel, bushy-tailed woodrat, and pinon mouse.

Along the combined elevation–precipitation gradient, approximately one half of the species absent from one or the other end of the gradient occurred on greater than one reach (Table 97). Species associations along this gradient reflected a combination of those of the elevation and precipitation gradients. Pinon mouse and Western gray squirrel were restricted to the lower end of the gradient, with Western gray squirrel only occurring in the lowest elevation and precipitation reaches. Two additional species, raccoon and vagrant shrew, were absent from the highest elevation and precipitation reaches. Bushy-tailed woodrat, mountain beaver, and brush mouse were restricted to the upper end of the gradient, with brush mouse occurring only in the highest elevation and precipitation reaches. Two additional species, ermine (*Mustela erminea*) and raccoon, were absent from the lowest elevation and precipitation reaches, reflecting their association with mesic and riparian habitats. Ermine was absent only along this gradient.

Finally, along the channel flow gradient most species were restricted to the lower end of the gradient, reflecting the negative relationship between alpha diversity and precipitation (Table 97). Only 1 of the 2 species restricted to higher channel flows occurred on more than one reach, broad-footed mole. The broad-footed mole is typically associated with riparian areas. Most of the 8 taxa associated with lower channel flows occurred on 2 or more reaches, and consisted of mountain beaver, brush mouse, pinon mouse, desert woodrat, bushy-tailed woodrat, and hares (*Lepus* sp.). All of these species, with the exception of mountain beaver, are typically associated with drier environments.

Species associations with the snag and log gradient were largely a reflection of the negative relationship between alpha diversity and woody debris (Table 98). Neither of the 2 species restricted to the upper end of the snag and log gradient were present on more than one reach. However 3 species were absent from reaches with the lowest density of snags and logs, consisting of porcupine, raccoon and pinon mouse. This may reflect an association with forested environments rather than an association with snags and logs. Most species were restricted to the lower end of the snag and log gradient. The 4 of the 6 species occurring only on the lower segments also occurred on more than one reach, and consisted of mountain beaver, brush mouse, and desert and bushy-tailed woodrat. Additionally, broad-footed mole and long-tailed weasel (*Mustela frenata*) were absent from reaches with the highest densities of snags and logs. This is the only gradient associated with the presence of long-tailed weasel.

TABLE 97. Mammal species present on 2 or more reaches and absent from lower or upper segments of each of 4 abiotic environmental gradient. Gradients were defined by principal components analysis. All taxa had a frequency of occurrence of  $\leq 10\%$ . Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Species	Elevation gradient				Precipitation gradient				Elevation-precipitation gradient				Channel flow gradient			
	low < ----- > high				low < ----- > high				low < ----- > high				low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Gray squirrel	X				X				X <sub>1</sub>							
Raccoon	X									X						
Vagrant shrew		X								X						
Pinon mouse		X			X <sub>1</sub>				X						X	
Brush mouse				X <sub>4</sub>				X <sub>4</sub>				X <sub>4</sub>			X	
Mountain beaver				X								X			X	
Bushy-tailed woodrat				X	X							X			X <sub>1</sub>	
Desert woodrat				X											X <sub>1</sub>	
Montane shrew					X											
Porcupine							X				X					
Ermine											X					
Hares													X			
Broad-footed mole							X									X
<i>Summary</i>	2	2	0	4	4	0	2	1	2	2	2	3	6	0	0	1

<sub>1</sub> Only occurs on segment 1.

<sub>4</sub> Only occurs on segment 4.

TABLE 98. Mammal species present on 2 or more reaches and absent from lower or upper segments of the snag and log gradient (derived by principal components analysis). All taxa had a frequency of occurrence of  $\leq 10\%$ . Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Species	Snag and log gradient			
	low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
Raccoon			X	
Brush mouse	X			
Pinon mouse			X	
Mountain beaver	X			
Desert woodrat	X			
Bushy-tailed woodrat	X			
Porcupine			X	
Broad-footed mole		X		
Long-tailed weasel		X		
<i>Summary</i>	<i>4</i>	<i>2</i>	<i>3</i>	<i>0</i>

I observed a range in the number of species absent from some portion of each of the 4 vegetation gradients (Table 99). About 50% of the species restricted to one end of the forest to meadow gradient occurred on 2 or more reaches. Only brush mouse and vagrant shrew were restricted to the meadow end of the gradient. Additionally, the broad-footed mole was absent from the most forested end of the gradient. Four species were restricted to the forested end of the gradient, including montane shrew, porcupine, pinon mouse and desert woodrat. Additionally, the bushy-tailed woodrat was absent from reaches with the most meadow. Typically, all of these species are associated with woody vegetation. An equivalent number of species were restricted to each end of the subalpine vegetation gradient, indicating high beta diversity. Two species were restricted to the upper end of the gradient: desert woodrat and bushy-tailed woodrat. Similarly, hares and pinon mouse were restricted to the lower end of the gradient. However, 4 additional species were absent from the upper most segment of the gradient: Western gray squirrel, broad-footed mole, vagrant shrew, and coyote (*Canus latrans*). The subalpine vegetation gradient is the only one associated with the presence of coyote, the only species absent from one or more segments and with a frequency of occurrence  $\geq 10\%$ . Only hares were restricted to the upper end of the alder–willow gradient. Raccoon and desert woodrat were restricted to the lower end of the alder–willow gradient. Along the aspen–cottonwood gradient, the brush mouse was restricted to the lower end of the gradient, and 3 species were restricted to the upper end of the gradient: broad-footed mole, montane shrew and desert woodrat.

TABLE 99. Species present on 2 or more reaches and absent from lower or upper segments of each of 4 vegetation gradients. Gradients were defined by principal components analysis. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Species	Forest to meadow gradient low < ----- > high				Subalpine vegetation gradient low < ----- > high				Alder–willow gradient low < ----- > high				Aspen–cottonwood gradient low < ----- > high			
	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only	Seg. 1&2 only	Seg. 1,2,3 only	Seg. 2,3,4 only	Seg. 3&4 only
<i>Frequency &lt; 10%:</i>																
Gray squirrel						X										
Raccoon									X							
Vagrant shrew				X		X										
Pinon mouse	X				X											
Brush mouse				X									X <sub>1</sub>			
Bushy-tailed woodrat		X						X								
Desert woodrat	X							X								X
Porcupine	X								X							
Hares					X							X				
Broad-footed mole			X			X										X <sub>4</sub>
Montane shrew	X															X <sub>4</sub>
<i>Frequency ≥ 10%:</i>																
Coyote						X										
<i>Summary</i>	4	1	1	2	2	4	0	2	2	0	0	1	1	0	0	3

<sub>1</sub> Only occurs on segment 1.

<sub>4</sub> Only occurs on segment 4.



### *Ranking Gradients for Beta Diversity*

The 8 environmental gradients were ranked to reflect their contribution to beta diversity based on the presence of mammal species (Table 100). The alder–willow gradient was ranked the highest contributor to species turnover, with a total turnover of 12 species, but only 3 of them were present on 2 or more reaches. It also had the highest average Whittaker’s beta diversity index. The elevation gradient was the second highest ranking gradient, followed by channel flow, snag and log, forest to meadow, subalpine vegetation, and aspen–cottonwood gradients. The combined elevation–precipitation gradient was not ranked in Table 100 because it was redundant with the individual elevation and precipitation gradients, however as a point of comparison it would have ranked first (total turnover = 12, core turnover = 9,  $\beta_{wMIN} = 0.125$ ) relative to the remaining gradients.

TABLE 100. Ranking of environmental gradients by their contribution to mammal beta diversity based on presence.

Environmental gradient	Total turnover	Core turnover - freq. $\geq 2$ reaches	Average $\beta_{wMIN}$	Rank
Alder–willow	12	3	0.146	1
Elevation	11	8	0.134	2
Channel flow	10	7	0.123	3
Snag and log	9	9	0.104	4
Forest to meadow	9	8	0.111	5
Subalpine vegetation	9	8	0.107	6
Aspen–cottonwood	8	4	0.104	7
Precipitation	7	7	0.084	8

### *Mammal Species Turnover by Basin Orientation*

Basin orientation influenced species turnover, as did the environmental gradients discussed above. All pair-wise comparisons of orientations were conducted to assess the contribution of basin orientation to species turnover (Table 101). Based on the average  $\beta_{wMIN}$  across all orientation comparisons, orientation had a relatively low contribution to beta diversity compared to the environmental gradients analyzed. All of the environmental gradients had higher average  $\beta_{wMIN}$  index values than orientation. The greatest species turnover occurred between the north and west orientations, with a minimum species turnover of 2 and a relatively high index value of 0.179. It was not possible to compare patterns of species turnover between basin orientation and the other gradients because orientations cannot be aligned along a linear gradient, however the comparison of east–dry and west–wet orientations provides a representation of all orientation comparisons, and the species turnover between these sides of the basin was low ( $n = 2$ ) (Table 101).

TABLE 101. Beta diversity index values for mammals among basin orientations. The number of species per segment, the number of species only occurring at upper (“gains”) or lower (“losses”) ends of the gradient, and Whittaker’s beta diversity index ( $\beta_w$ ) are displayed. A modified version of Whittaker’s beta diversity index ( $\beta_{wMIN}$ ) is also displayed. N = north, E = east, S = south, W = west side of the basin. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Basin orientation	Richness of first segment	Richness of second segment	Total richness	Gains	Losses	$\beta_w^*$	$\beta_{wMIN}^\dagger$
N:E	28	33	33	5	0	0.082	0.000
E:S	33	19	34	1	15	0.308	0.030
S:W	19	26	26	7	0	0.156	0.000
N:S	28	19	29	1	10	0.234	0.036
E:W	33	26	35	2	9	0.186	0.061
N:W	28	26	33	5	7	0.222	0.179
<i>average</i>							<i>0.051</i>
<i>N and E:S and W</i>	<i>33</i>	<i>26</i>	<i>35</i>	<i>2</i>	<i>9</i>	<i>0.186</i>	<i>0.061</i>

\* Whittaker’s beta diversity index:  $S/\alpha - 1$ , where  $S$  = total species richness, and  $\alpha$  = the average species richness of the two segments being compared.

† Modified Whittaker’s beta diversity index:  $(S/s\text{-max}) - 1$ , where  $S$  = total species richness, and  $s\text{-max}$  = the highest richness of the two segments being compared, resulting in a minimum beta diversity value.

Species absent from one or more orientations provide species specific contributions to the gains and losses observed between orientations. Fourteen species occurring on more than one reach were absent from one or more orientations (Table 102). The south side of the basin had the greatest number of species absent ( $n = 12$ ), followed by the west side of the basin ( $n = 8$ ), consistent with the high alpha diversity associated with the north and east sides of the basin. Contributing to this pattern were the 6 taxa occurring only on the north or east sides of the basin. Species appeared to differentiate between the more xeric orientations (north and east) and the more mesic orientations (south and west). For example, bushy-tailed woodrat, desert woodrat, pinon mouse, mountain beaver, and hares were only observed on the north and east sides of the basin. Alternatively, porcupine was only observed on the south and west sides of the basin. A shrubby and rocky environment associate, the brush mouse, was only observed on the north side of the basin. Additional evidence that mammal species segregated based on the moisture regime comes from the species with only one detection. Nuttall’s cottontail (*Sylvilagus nuttallii*) was observed only on the north side, least chipmunk and Belding’s ground squirrel (*Spermophilus beldingi*) were observed only on the east side, whereas the water shrew (*Sorex palustris*) was observed only on the west side of the basin. The 3 species observed on the north and east sides are associated with more xeric conditions, whereas the water shrew is associated with mesic environments (Zeiner et al. 1990b).

TABLE 102. Mammal species occurring on more than one reach and absent from one or more basin orientations. X's indicate where species was present. Sample reaches per orientation are indicated. Data were collected on sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Species	Presence by basin orientation			
	Xeric < ----- > Mesic			
	North ( $n = 20$ )	East ( $n = 20$ )	South ( $n = 16$ )	West ( $n = 24$ )
<i>Frequency &lt; 10%:</i>				
Brush mouse	X			
Bushy-tailed woodrat	X	X		
Desert woodrat	X	X		
Mountain beaver	X	X		
Pinon mouse	X	X		
Hares	X	X		
Ermine	X	X		X
Broad-footed mole	X			X
Gray squirrel	X		X	X
Montane shrew		X		X
Vagrant shrew		X		X
Raccoon		X		X
Porcupine			X	X
<i>Frequency <math>\geq 10\%</math>:</i>				
Shadow chipmunk	X	X		X
<i>Sum of absent species</i>	<i>4</i>	<i>3</i>	<i>12</i>	<i>8</i>

### *Concordance Among Diversity Measures*

#### *Measures of Alpha Diversity*

All measures of richness (total richness, richness by habitat group, and richness by frequency class) were positively correlated with each other (Table 103). Both frequency classes were positively correlated with both habitat groups. Reviewing the species associated with each grouping revealed that 66% of the 12 aquatic-riparian-meadow-associated species were rare, and over 50% of the upland associates were rare. A similar pattern held for rare and common species, where aquatic-riparian-meadow-associates comprised 25 to 30% of each habitat group. This intermixing is a function of the high number of species identified as rare (66%).

TABLE 103. Correlations among measures of mammal alpha diversity. Bolded values indicate  $P \leq 0.05$ . Shading indicates redundant cells. Data were collected at sample reaches ( $n = 80$ ) in the Lake Tahoe basin, 1995 to 1996.

Mammal richness measures	Taxonomic richness		Aquatic–riparian–meadow-associated species richness		Upland-associated species richness	
	r	P	r	P	r	P
Taxonomic richness						
Aquatic–riparian–meadow associates	<b>0.550</b>	<b>&lt;0.001</b>				
Upland associates	<b>0.877</b>	<b>&lt;0.001</b>				
Rare species	<b>0.646</b>	<b>&lt;0.001</b>	<b>0.465</b>	<b>&lt;0.001</b>	<b>0.499</b>	<b>&lt;0.001</b>
Common species	<b>0.748</b>	<b>&lt;0.001</b>	<b>0.359</b>	<b>0.001</b>	<b>0.692</b>	<b>&lt;0.001</b>

### *Alpha and Beta Diversity*

An average of 24.6 (range = 22 to 28, SE = 0.29) mammal species were shared among segments ( $n = 20$  reaches per segment), based on segment comparisons across all environmental gradients. The average richness lost or gained between segments was 2.7 species (range = 1 to 8, SE = 0.31), and it was not significantly different (based on paired t-test across gradients,  $P = 0.368$ ) than the average number of species turnovers between segments ( $\bar{x} = 3.1$  species, range = 1 to 6, SE = 0.24). The average number of species shared among segments constituted 70.3% of all species observed, and variation in richness and species turnover constituted 7.7% and 8.9%, respectively, of all species observed.

The analysis of the relative influence of environmental gradients on gamma diversity in the basin showed that the channel flow and alder–willow gradients had the greatest contribution to gamma diversity in the basin (Fig. 42). The channel flow and alder–willow gradients showed shifts of 16 and 15 species, respectively, along their lengths, comprising approximately 43% of the total mammal fauna. The diversity associated with the alder–willow gradient was primarily driven by species turnover, whereas a greater balance of shifts in richness and turnover were associated with the channel flow gradient. These 2 gradients were followed in their contribution to diversity by subalpine vegetation, which was very similar to the channel flow gradient, with just one fewer species shifting along its length. Snags and logs, and elevation followed subalpine vegetation, with 12 and 11 species, respectively, shifting in association with these gradients. Diversity associated with the snag and log gradient was driven primarily by species turnover, and it was entirely responsible for the observed diversity associated with elevation. Forest to meadow, aspen–cottonwood, and precipitation gradients all had a total change in species composition of 10, and the change was primarily attributed to beta diversity. The difference in compositional change among the gradients ranged as high as 7 species--20% of the observed total species richness.

The total change in composition was more closely correlated with alpha diversity ( $r = 0.723$ ,  $P = 0.043$ ) than beta diversity ( $r = 0.516$ ,  $P = 0.190$ ), and the individual contributions of alpha and beta diversity were not correlated ( $r = -0.219$ ,  $P = 0.602$ ). In general, net changes in richness (alpha diversity) along gradients were lower and more variable ( $\bar{x} = 2.9$ , SE = 0.69) than changes in composition (beta diversity) ( $\bar{x} = 9.3$ , SE = 0.56).

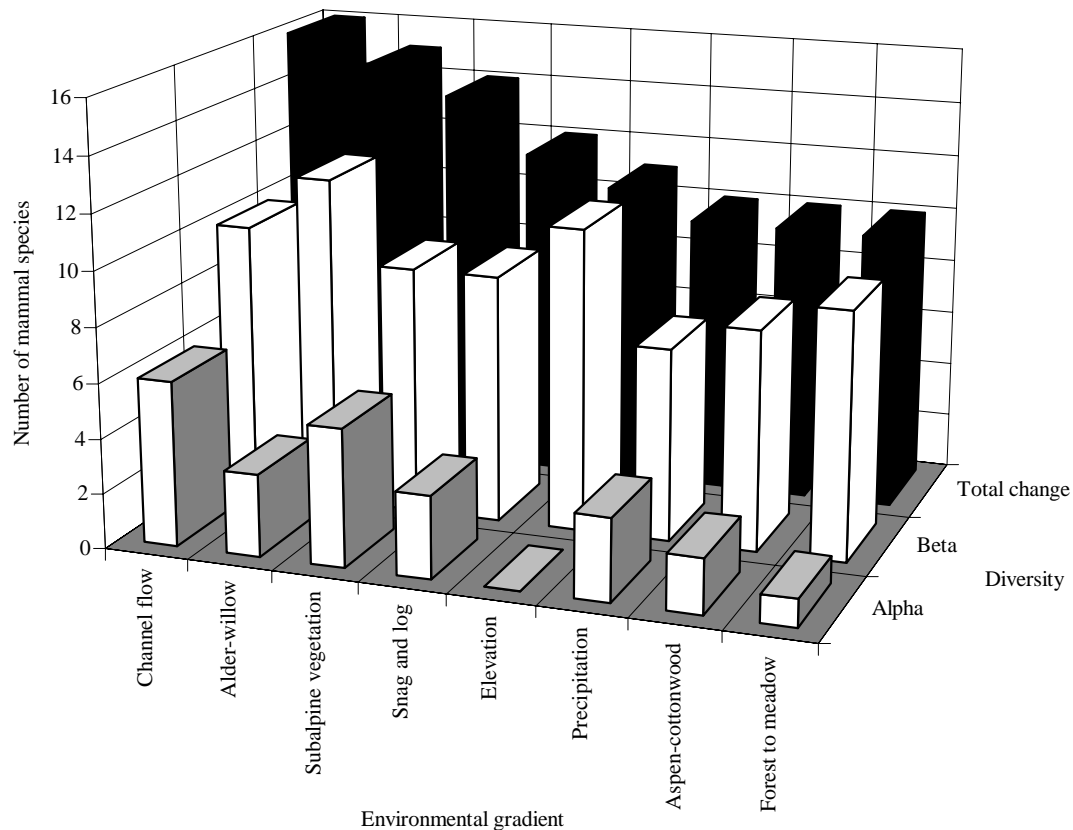


FIG. 42. Contribution of each of 8 environmental gradients to mammal diversity in the Lake Tahoe basin. Total change in composition is shown, along with the composite contributions of alpha and beta diversity. Data were collected on 80 sample reaches, 1995 to 1996.

## DISCUSSION

### *Environmental Influences on Mammal Diversity*

I encountered a high richness of 35 species of mammals, of which approximately 35% were aquatic, riparian, or meadow associates. Although reaches ranged widely in environmental conditions, they shared many species, with any given reach containing an average of 26% and as high as 49% of the total number of mammal species observed throughout the Lake Tahoe basin. Concomitantly, turnover was relatively low, ranging from 6 to 14% from the lower to upper ends of the 8 environmental gradients examined. Therefore, environmental features that affect alpha diversity (patterns of richness per reach) and rare species are the most potent influences on the diversity of mammals in the Lake Tahoe basin. Seven species (20% of all species) occurred on > 50% of all reaches, thus these species formed the base composition of most reaches. The remaining species were present on < 25% of the reaches, and these less common species were responsible for variation in per-reach richness and contributed the most to variation in alpha diversity, as well as beta diversity.

Aspen-cottonwood, lodgepole pine, and elevation were the environmental features most strongly associated with the higher richness of mammals. Aspen-cottonwood and lodgepole pine supported more rare species, whereas upper elevations supported more common species.

All measures of richness, with the exception of common species richness, increased with increases in aspen–cottonwood, and at least 6 mammal species were observed where aspen–cottonwood occurred.

Although aspen–cottonwood was positively associated with richness, many reaches without aspen–cottonwood had high species richness, including a reach with the second highest richness of mammals ( $n = 16$  species). Lodgepole pine, the other environmental feature associated with increased richness of rare species, rarely ( $n = 3$  reaches) co-occurred with aspen–cottonwood. Thus, at upper elevations where lodgepole pine was more common than aspen–cottonwood, rare species were richest in association with lodgepole pine.

In contrast to aspen–cottonwood and lodgepole pine, total richness and the richness of common species increased with elevation. The dominant role of common species in higher mammal richness at upper elevations was evidenced by the threshold observed at 2250 m in elevation, above which a minimum of 5 species per reach were upland or common. However, patterns of richness in association with elevation were not entirely straightforward. Although richness generally increased with elevation, the number of species per elevation segment ( $n = 20$  reaches) did not vary substantively among segments from low to high elevation. Upon closer examination, it was apparent that the increases in richness associated with elevation reflected a slightly greater richness of species occurring at higher elevations combined with an increased frequency of occurrence per species on higher elevation reaches. Thus, mammal species were more ubiquitous at higher elevations.

Although a low number of species turned over along gradients, they nevertheless represented a large proportion of the mammalian fauna, and thus environmental gradients associated with the greatest beta diversity had substantial effects on diversity of certain taxa. The contribution of turnover to the diversity of mammals in the Lake Tahoe basin was associated with a few gradients, namely elevation and alder–willow. Elevation was unique in its association with both richness and turnover, and had the second highest turnover of any environmental gradient. A high proportion (25%) of all mammal species occurring on more than one reach were restricted to lower or higher elevation reaches. Mammal richness was variable and turnover was relatively high along the subalpine vegetation gradient, which was closely associated with elevation. These results suggest that elevation created a strong gradient of environmental conditions supporting a diversity of mammal species. Although many high elevation associates were common, habitat specialists such as shadow chipmunk and ermine were also associated with higher elevations.

Species composition also changed substantially along the alder–willow gradient, and in contrast to elevation, rare species were primarily responsible for the high turnover. High turnover of rare species, combined with a slight decline in species richness (i.e., 3 fewer species at the upper end of the gradient), resulted in alder–willow having a major effect on the composition of mammals in the Lake Tahoe basin.

Channel flow gained distinction as a major contributor to diversity as a result of the combined contributions of alpha and beta diversity. Changes in species composition were greater at the lower end of the channel flow gradient, being driven at least in part by opposing relationships between upland species (associated with low channel flow), and aquatic–riparian–meadow species (associated with high channel flow). The shift toward aquatic–riparian–meadow species in association with higher channel flow was accompanied by a loss in species richness. For example, the abundance of one common species (long-tailed vole), was positively correlated with channel flow, whereas the abundance of 3 common species (yellow-pine chipmunk, shadow chipmunk, and golden-mantled ground squirrel) were negatively correlated with channel flow. Overall, the relationships of species along this gradient indicate that various channel flow conditions offer a diversity of resources which in turn supports a diversity of mammal species.

Orographic effects on mammal species were substantial, given that mammal richness varied significantly and turnover was high among basin orientations. Orientation appeared to integrate

the array of environmental features acting on the occurrence and distribution of mammals in the Lake Tahoe basin, such as elevation, precipitation, spatial heterogeneity, and topography. All measures of diversity varied by orientation, with the exception of rare species richness and total abundance. The east side of the basin, and the north side to a lesser extent, appeared to provide a highly suitable combination of lower elevation, drier areas dominated by upland forest vegetation, such as mixed conifer, and a relative abundance of aspen–cottonwood, which supported a high richness of common and upland mammal species. As expected, most of the 7 species restricted to the north or east side of the basin (e.g., brush mouse, woodrats, pinon mouse, hares) are associated with drier environments. In contrast, aquatic–riparian–meadow species were most speciose in association with the more mesic conditions on the west side of the basin.

### *Individual Species and Species Groups*

The investigation of aquatic–riparian–meadow-associated species and rare species was helpful in discerning environmental features of relevance to these important subsets of species. Both habitat groups (aquatic–riparian–meadow and upland associated species) were highly related to environmental conditions described in this study. This suggests that most mammal species, regardless of their environmental affiliation, use riparian environments for some aspect of their life history (e.g., cover, feeding, resting, reproduction, thermoregulation).

It was obvious that the most commonly occurring species highly influenced the environmental relationships exhibited by taxonomic richness. For example, total species richness was not associated with meadow, mixed conifer, or the forest to meadow gradient. However, the richness of aquatic–riparian–meadow associates and upland associates had opposing relationships with meadow, mixed conifer, and the forest to meadow gradient. Rare species richness was also associated (positively) with the forest to meadow gradient. As such, analysis of species groups revealed that the primary vegetation gradient (forest to meadow) supported a mammalian gradient (aquatic–riparian–upland species), and that meadow and lodgepole pine habitats provided habitat for a large proportion (60% of the mammal assemblage was rare) of the mammalian fauna in the Lake Tahoe basin. The importance of the forest to meadow gradient in supporting such a diversity of species was not obvious in patterns of total species richness, and would have been overlooked if patterns of subsets of species had not been explored.

Mammal diversity is expected to be related to the structural and compositional diversity of vegetation based on the results of previous studies (e.g., Dueser and Shugart 1978, Swihart and Slade 1990, Williams 1997, Schweiger et al. 1999). However, in my study the abiotic influence of channel flow, along with meadow, strongly differentiated the richness of aquatic–riparian–meadow associates from upland associates. Aquatic–riparian–meadow associates were most speciose in association with high channel flow conditions and open, meadow environments, with mountain pocket gopher, long-tailed vole, and montane vole being among the most frequently occurring aquatic–riparian–meadow-associated species. Conversely, upland associates were most speciose in association with low channel flow conditions and forested environments. The richness of common species was also closely correlated with abiotic conditions, increasing with lower channel flows, upper elevations, and a lower abundance of meadow, with deer mouse, long-eared chipmunk, Douglas squirrel, and California ground squirrel being the most frequently occurring upland-associated species.

A number of species exhibited limits in regard to one or more environmental gradients,

including the alder–willow, elevation, subalpine vegetation, and snag and log gradients. The greatest number of species was absent from some portion of the alder–willow gradient, including raccoon, porcupine, hares, and mountain pocket gopher. The raccoon and porcupine were present only in areas with a low proportion of alder–willow. The raccoon is considered a habitat generalist, but is often associated with riparian or wetland areas (Verner and Boss 1980). However, the raccoon is above its typical elevational range in the Lake Tahoe basin (Storer and Usinger 1963, Whitney 1979, Hall 1995), and the structure and abundance of alder–willow at higher elevations may pose a barrier to raccoon movement or foraging. The porcupine is a moderate habitat specialist, associated with various ages of conifer forest. At the other end of the gradient, the occurrence of hares where alder–willow was more abundant is indicative of a habitat specialization. Alder–willow may provide valuable cover (Zeiner et al. 1990b) and a winter food source (Wolff 1980) for hares, particularly in the higher elevations in which they occur. Finally, the abundance of mountain pocket gopher increased with alder–willow, indicating favorable soil characteristics or perhaps food resources in the form of roots of alder–willow or associated plant species (Zeiner et al. 1990b).

Four mammal species exhibited limits along the elevation and subalpine vegetation gradients: ermine, gray squirrel, raccoon, and coyote. The ermine was absent from the lowest elevation reaches. The ermine is known to occupy a range of elevations, but was noted by Orr (1949) to occupy only the higher elevations in the Lake Tahoe basin. The higher elevation occurrence of ermine could be the result of competitive exclusion induced by its larger congener, the long-tailed weasel. In contrast, the gray squirrel and raccoon were absent from higher elevations, and the coyote and gray squirrel were similarly absent from the upper most segment of the subalpine vegetation gradient. Gray squirrel and raccoon are above their typical elevational limit in the Lake Tahoe basin, and appear to be restricted to the lower elevations (and associated vegetation types) in the basin. The coyote is a common species in the Lake Tahoe basin and a habitat generalist, but food resources may be more limited at higher elevations and winter movement more difficult where snow packs are deeper. The abundances of larger-bodied prey of the coyote, specifically the California ground squirrel and long-eared chipmunk, were negatively associated with subalpine vegetation, and therefore the abundance of these species may be influencing the distribution of the coyote (Gese et al. 1996, Quinn 1997).

The long-tailed weasel was absent from reaches with the highest densities of snags and logs. The long-tailed weasel is known to forage in more open habitats, and preys primarily on voles and mice, as well as chipmunks, gophers, and squirrels (Zeiner et al. 1990b). Although the abundance of deer mouse, perhaps its most abundant prey item, was positively associated with snag and log densities, it may be that reaches with low to moderate density snags and logs provide the most favorable balance of abundant and accessible prey.

### ***Conservation and Management Implications***

The high diversity of mammals in the Lake Tahoe basin is evidenced by lower richness estimates from other studies in similar environments. McComb et al. (1993) studied small mammal communities in alder-dominated habitats in Oregon, and detected a total of 24 species using both Sherman and pitfall traps. Gomez and Anthony (1998) detected 20 species of mammals based on pitfall traps alone in their study of mammal composition in upland and riparian conditions in Oregon. Keane and Morrison (1994) studied small mammals in portions of the Lake Tahoe basin and detected 14 species of small mammals using Sherman traps. It is likely that the number of species I encountered was higher than these other studies in part because of the sampling intensity and combination of methods (Sherman trapping, pitfall trapping, and



riparian searching) I employed. Relative to Sherman trapping alone, I sampled for a total of 25,900 trap nights, whereas McComb et al. (1993) and Keane and Morrison (1994) sampled for 4800 and 7211 trap nights, respectively. However, a large proportion of the genera, over 1/3 ( $n = 7$ ), were represented by 2 to 5 species. This high preponderance of congeners is likely to be the result of the strong elevational gradient and the location of the basin at the interface of 2 zoogeographic regions.

The geographic location and topographic configuration of the Lake Tahoe basin converge to create a unique faunal interchange between zoogeographic regions, which is reflected in the distribution of mammal species in the basin. The east side of the basin lies along this transition from fauna associated with the Sierra Nevada zoogeographic region to fauna associated with the Great Basin zoogeographic region (Udvardy 1969, 1975), and a mix of species from each region occurred in the Lake Tahoe basin. These influences were expressed in the difference in species composition observed between the north and east orientations and south and west orientations. The Lake Tahoe basin is a unique faunal area within Nevada (Hall 1995), meaning species that typically occur only on the west side of the Sierra Nevada crest are found throughout the basin, including that portion occurring in Nevada. For example, Sierra Nevada-associated species such as long-eared chipmunk, bushy-tailed woodrat, Douglas squirrel, and mountain pocket gopher were found on the Nevada (east) side of the basin along with desert-associated species, such as least chipmunk, Nuttall's cottontail, and desert woodrat. When conservation is directed at a species (species-based), maintaining populations that occur on the edge of the species range may not be as high a priority because they may not be considered critical to the long-term viability of the species. However, when the objective is to conserve biological diversity in a particular location (place-based) different considerations apply. In the Lake Tahoe basin, almost half of the mammal species are at the east–west edge of their range, and persistence of their populations is critical to maintaining mammal diversity in the basin.

The greater frequency of occurrence of species, combined with no substantive change in the number of unique species, at higher elevations could be explained by a combination of a few phenomenological influences. A parsimonious explanation is that environments commonly occurring at higher elevations are more homogeneous (composition and structure) and suitable to most species occurring at these higher elevations. Environmental homogeneity is likely to be partially responsible for the observed patterns of richness, yet it does not explain why the number of unique species did not decline with elevation. Declines in mammal species richness with elevation have been observed by a number of researchers (e.g., Abramsky and Rosenzweig 1984, Heaney and Rickart 1990, Williams 1997). The lack of an observed decline in richness with elevation could reflect a depauperate fauna at lower elevations induced by topographic isolation of the Lake Tahoe basin. More likely, this pattern is the result of human disturbance (primarily urbanization), which is more prevalent at lower elevations. Further experimental studies are needed to confirm this hypothesis.

The topographic isolation of the Lake Tahoe basin could be inducing a reduced richness of mammal species at lower elevations, particularly along the higher Sierra crest which defines the western boundary of the basin. Fauna at the lowest elevations in the basin would normally be enriched by species associated with even lower elevations. However, the Lake Tahoe basin is surrounded by mountain crests, with only a few topographic saddles as low as 2100 m. Species that could persist at lower elevations within the basin (e.g., gray fox [*Urocyon cinereoargenteus*], bobcat [*Lynx rufus*]) may be absent because topographic barriers prevent these species from immigrating into the basin or suitable habitat is too limited to support populations once they arrive. Lomolino et al. (1989) found that the richness of montane forest mammals was lower in relation to the degree of isolation of forest patches. Similarly, Terborgh and Weske (1975) found that isolated high elevation sites in Cerros del Sira in the Andes had a depauperate bird fauna

compared to high elevation sites that were part of a contiguous mountain chain. They found that isolation resulted in lower numbers of high elevation associates, as well as the presence of some lower elevation species that would typically be out competed by high elevation specialists. These studies illustrate that topographically isolated faunas may lack species that would normally occur in similar habitats located in contiguous habitat configurations.

Species composition and rarity provide some evidence of topographically-induced reduction in species richness is present. A number of species are rare or absent in the Lake Tahoe basin that might otherwise be more common if the basin were not topographically isolated. Six mammal species of the Sierra Nevada mountains (gray fox, dusky-footed woodrat [*Neotoma fuscipes*], ringtail [*Bassariscus astutus*], bobcat, striped skunk [*Mephitis mephitis*], and spotted skunk [*Spilogale putorius*]) reach their elevational limits between 1800 m and 2100 m, and most are absent within the Lake Tahoe basin even though their elevational ranges extend above the lowest elevations in the basin. These species have the potential to exist in the Lake Tahoe basin, and may establish populations periodically over time, but are particularly vulnerable to extirpation because of small population sizes and ostensibly low immigration rates. Management should consider the potential impacts of the timing and location of management activities on rare species, particularly species thought to be at the edge of their range or ecological niche (Grinnell 1917, Elton 1927, Gause 1934, Hutchinson 1957), and with potentially limited immigration rates.

Human disturbance within the Lake Tahoe basin is substantial, and it is greater at lower elevations, in proximity to Lake Tahoe. Human disturbance includes conversion of natural environments to buildings and parking lots, fragmentation of natural environments by roads and rural communities, direct human disturbance from hikers, bikers, and motorized vehicles, and disturbance from livestock grazing. Fragmentation can affect mammal species richness and abundance as demonstrated by various studies (e.g., Gains et al. 1992, Robinson et al. 1992, Diffendorfer et al. 1995, Commons and Barrett 1997). In addition to human-induced fragmentation, riparian environments in the Lake Tahoe basin are inherently fragmented because the majority of watersheds in the basin are small, they have subterranean flows in some sections, and the steep elevational gradient induces relatively rapid shifts in vegetative communities within watersheds from mouth to headwaters. Although the management emphasis in the Lake Tahoe basin is to protect and restore riparian environments (USDA 1988), human impacts are still a potential threat to the quality of riparian environments. The protection of riparian environments from degradation (e.g., fragmentation), and facilitating the ability of populations to reestablish if local extirpations were to occur are important conservation considerations in planning and managing for mammal diversity in the basin.

Alder–willow contributed substantially to supporting mammal diversity in the basin. A range of densities of alder–willow may increase the spatial heterogeneity of resources across reaches thereby providing habitat for a greater number of species. Alder–willow vegetation is typically considered a highly productive environment capable of supporting a high vertebrate diversity because of their association with water and because deciduous trees are associated with high food resources (i.e., edible plant material and associated phytophagous insects) (Grenfell 1988). Alder and willow occurred frequently (96% of all reaches) along stream reaches, and was generally well-distributed throughout the Lake Tahoe basin. Management activities are unlikely to change the distribution of alder and willow, however grazing and channel restoration could alter its abundance. Species closely associated with alder and willow, such as the mountain pocket gopher, could additionally be directly impacted by livestock grazing through soil compaction and trampling. Channel restoration could restore alder–willow vegetation where it has known to be reduced or lost, but it could also negatively affect the distribution and abundance alder and willow. Restoration efforts in areas with well-developed alder and willow

vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow environments.

The greatest variation in vegetation occurred at low to mid elevations from forest to meadow, and it was paralleled by a turnover in composition from upland-associated species to aquatic–riparian–meadow-associated species. Both meadow and mixed conifer forest offer a rich array of resources, but they differ greatly in the kinds of resources found in each type. Meadows are structurally simple but highly productive environments, whereas mixed conifer forests are structurally complex and have an abundance of forest associated resources such as conifer seeds and woody material. The management of meadows and mixed conifer forests, particularly those at mid to low elevations, could have significant effects on the richness of aquatic, riparian, and meadow associated mammals. The greatest potential impacts to mixed conifer forests are the lack or mismanagement of fire (prescribed and wildfire), timber harvest, and recreation disturbance. The greatest threats to meadow condition and extent are lack of fire, which can affect succession, and water diversions and grazing, which can affect the hydrodynamics of meadows (Ratliff 1985). Agencies within the Lake Tahoe basin are increasing the use of prescribed fire in an attempt to restore the function of fire in reducing flammable fuels. Prescribed fires and wildfires that are allowed to burn, and timber harvested with the intent of mimicking natural processes (e.g., fire, disease, windthrow), should generally improve the quality and quantity of vegetative conditions in the basin. Water diversions are rare in the Lake Tahoe basin, but channel restoration efforts are relatively common (TRPA 1997), and such efforts should consider potential impacts on meadow systems.

Lodgepole pine is typically considered a low diversity environment because of its simple vertical structure (Verner and Boss 1980). However, in the Lake Tahoe basin, it appears that lodgepole pine plays an important role in the supporting mammal diversity, particularly in supporting rare species. Adjacent to streams, as in this study, the understory of lodgepole pine typically consists of grasses, forbs, and sedges (Bartolome 1988, Potter 1994). Any effort to conserve the richness and diversity of aquatic, riparian, and meadow mammal species in the Lake Tahoe basin would benefit from special management considerations for lodgepole pine in proximity to streams and meadows. Potential management impacts include cattle grazing and fire management.

Woody debris can be a benefit or a detriment to mammal diversity in the Lake Tahoe basin, depending on its dimensions and abundance. On one hand, positive relationships were observed between logs and the richness and abundance of upland and common species. Downed woody debris in the form of logs provides a variety and abundance of resources for small mammals, including cover (e.g., nesting, denning, protection from predators), food (e.g., associated invertebrates and fungi), and utility as runways to facilitate movement through the forest (e.g., Maser et al. 1979, Maser et al. 1981, Carey and Johnson 1995). However, negative relationships were also observed between mammal richness and high snag and log densities, indicating that mammal diversity did not benefit from the highest snag and log densities. For logs, this equates to an approximate average of over 230 m/ha of large logs and 450 m/ha of small logs. A high density of small snags and logs occur in the Lake Tahoe basin as a result of recent large-scale tree mortality events (Weatherspoon et al. 1992, McKelvey et al. 1996, Manley et al. 2000), as evidenced by the high frequency of occurrence (> 80%) of large snags and both sizes of logs across all sample reaches. Existing stands of dense, small diameter snags and logs had low suitability for some mammal species. Logs must be a minimum diameter to provide particular functions, such as providing runways for small mammals or harboring food resources for black bears (Maser et al. 1979). Management of woody debris to benefit mammal diversity should focus on the retention and recruitment of large logs. Attempts to reduce fine fuels in the Lake Tahoe basin may reduce the density of small snags and logs, but may also pose a risk to the

quality and quantity of large snags and logs. Charring may reduce the suitability of snags and logs for wildlife species. The management of forests through timber harvest, fuelwood harvest, and fire should consider their impact on log quantity and quality for the benefit of mammal diversity.

Canopy cover was not associated with total richness or abundance, but it appeared that the potential richness of aquatic–riparian–meadow associates was reduced by one half (from 6 to 3 species per reach) where canopy cover index was < 40%. The relationship between aquatic–riparian–meadow species richness and canopy cover probably reflects vegetative conditions, such as meadow and open-canopied lodgepole pine versus physiological constraints such as temperature, shade, or cover. However, canopy cover could potentially serve as an index of habitat suitability for the richness of aquatic–riparian–meadow species.

Aspen–cottonwood had a significant association with the alpha diversity of mammals, particularly rare species. A variety of mammal species are known to use aspen for cover, nesting, thermal insulation, and foraging. Young stands of aspen, especially during fall and winter when protein content of aspen is high relative to other shrub species, provides forage for mule deer (*Odocoileus hemionus*) (Tew 1970, Bartos and Johnson 1978). Black bear (*Ursus americanus*) forage on berry-producing plants and forbs that establish in the understory of aspen stands. Aspen groves also provide bear with suitable denning sites (DeByle 1985). Rabbits, hares, and pikas (*Ochotona princeps*) eat quaking aspen buds, twigs, and bark year-round (Brinkman and Roe 1975, DeByle 1985). Small rodents, including squirrels, pocket gophers, mice, and voles feed on aspen during at least part of the year (Jones and DeByle 1985). Pocket gophers are commonly present in aspen stands (DeByle 1985). The highest densities of rodents in aspen stand tend to occur in mature stands (Probst and Rakstad 1987).

High alpha diversity of mammals in aspen–cottonwood suggests a combined influence of a structurally complex environment (understory and overstory) and a high productivity environment (DeByle and Zasada 1980). In the Lake Tahoe basin, aspen and cottonwood are among the few dominant deciduous trees. Deciduous trees, particularly riparian-associated trees, offer a rich source of resources to many animals, including invertebrates and vertebrates (Whitney 1979, DeByle 1985, Grenfell 1988, Verner 1988). The mesic sites that permit aspen to establish also result in higher insect production compared to adjacent evergreen forests or shrublands (Winternitz 1980). The fact that aspen–cottonwood was so strongly associated with mammal richness despite its rarity in the study area (and throughout the Lake Tahoe basin) suggests that this vegetation type serves a pivotal role in supporting mammal diversity. Mammal species detected in this study expected to be closely associated with aspen–cottonwood include mountain pocket gopher, porcupine, black bear, mule deer, and deer mouse (DeByle 1985).

Given the substantial contribution of aspen and cottonwood to mammal diversity in the Lake Tahoe basin, it provides the greatest opportunity of any riparian woodland vegetation type for enhancing habitat values for riparian-associated mammal species in the Lake Tahoe basin. Aspen stands are sometimes ephemeral vegetation associations which are succeeded by conifer forests in the absence of fire. However, depending on soils and moisture, some aspen stands can be relatively permanent features even in the absence of fire (Barry 1971, Youngblood and Mueggler 1981, Mueggler and Campbell 1982). In the Lake Tahoe basin, it is possible that the lack of fire has reduced the extent of aspen. The increased use of prescribed fire and proportion of wildfires that are allowed to burn are likely to improve the vigor and perhaps the extent of aspen stands in the basin.

Channels with lower gradients and wider channels supported a greater richness of aquatic–riparian–meadow-associated mammals than smaller, steeper channels. Mammal diversity, and aquatic–riparian– meadow associates in particular, were expected to be positively

correlated with channel flow because wide, low gradient stream reaches have increased floodplain width, gentler topography, milder microclimates, and more well-developed riparian vegetation in proximity the stream (Vannote et al. 1981, Gregory et al. 1991). However, common species (comprised of 70% upland species) showed a strong negative association with channel flow characteristics. Upland environments generally provide an abundance of resources for the majority of mammal species, including resources such as conifer seeds (chipmunks, squirrels, mice), fungi (flying squirrel), conifer trees (porcupine), and shrubs (deer, bear, mice) (Zeiner et al. 1990b). The opposing relationships observed between upland and aquatic-riparian-meadow-associated species in regard to channel gradient and width indicate that these channel characteristics greatly influenced diversity.

Mammal species richness varied within and among gradient segments, and in some instances these two sources of variation showed opposing patterns of association with the gradient, as observed along the elevation gradient. In this study, changes in the frequency of occurrence of species along the elevation gradient created the appearance of increased richness at higher elevations. Changes in frequency of occurrence can exaggerate or create apparent trends in species richness (as observed in this study between richness and elevation), or they can mask trends in richness if frequency of occurrence increases as richness per site decreases. The potential for species frequency of occurrence to change along a gradient is probably greatest for gradients that are strongly associated with primary factors known to affect species occurrence, such as productivity or spatial heterogeneity. My study results suggest that survey or monitoring efforts need to analyze patterns in richness and composition at more than one spatial scale to obtain an accurate depiction of relationships between diversity and environmental gradients.

The conservation of specialists, rare species, orographically constrained or environmentally restricted species is a critical element of any effort to conserve biological diversity. Patterns of richness and turnover provide valuable insights into environmental features that support the majority of species. The concept of a coarse-filter approach to conservation, developed by the Nature Conservancy (Noss 1987), would apply well in the case of conserving the majority of stream-associated mammal species in the Lake Tahoe basin because of the high per-reach richness observed. The coarse-filter approach would entail conserving a breadth of vegetation and aquatic community types without specific attention paid to the species associated with each. Fine-filter conservation approaches complement coarse-filter approaches by considering additional environmental requirements for species that are not supported by a coarse-filter approach (Noss and Cooperrider 1994). Fine-filter approaches focus on species that are specialists, rare, geographically restricted, or declining in numbers (Noss and Cooperrider 1994).

The individual species identified as potential specialists, as well as species considered rare, or limited to 1 to 2 basin orientations, are good candidates for individual conservation considerations. For example, certain orientations may offer the only suitable habitat for some species of mammals (e.g., east side). The location, distribution, and timing of conservation actions (e.g., water development projects, control of exotics) and management treatments (e.g., prescribed fire, timber harvest, road building) should take into consideration the potential impacts on geographically limited species. Species known to be declining in numbers were not specifically addressed in this study, but obviously they should also be included in the development of any fine-filter conservation approach.